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Genetic Variation in Douglas-fir: A 20-year Test of Provenances in Eastern Nebraska

David F. Van Haverbeke



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Abstract

Twenty-year-old Douglas-fir trees in provenances from Arizona, New Mexico, and southern Colorado survived better and grew taller; but incurred more winter injury in eastern Nebraska than trees from provenances from northern Colorado, southern and western Montana, northern Idaho, Canada, and eastern Washington. However, surviving trees from Pacific Coast, and northern and central Rocky Mountain provenances increased in percent of plantation mean height during the past 9 years, whereas trees from southern Rocky Mountain provenances decreased. Age/age correlations indicate provenances expressing superior height growth can be identified at age 6.

Acknowledgements

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Management Implications

Douglas-fir is a conifer species that is not indigenous to the Great Plains. However, it has been planted sparingly and in selected locations, mainly as an ornamental, throughout the central Great Plains for many years. Interest in its use for Christmas trees has increased in recent years.

Identification of seed sources of Douglas-fir that are adapted to the central Great Plains environment could increase its use, reduce planting failures, and add to the number and variety of conifer species available to forestry agencies and commercial nurseries for wind-breaks, Christmas trees, and environmental and esthetic plantings within the Great Plains—a region in which few conifer species are native.

Cautionary Statement

Heavy mortality in the nursery and during the first year of field establishment imposed severe limitations on the analysis and interpretation of 20-year-old Douglas-fir provenance data. Numbers of individuals in some provenances, particularly those of northern origin, were reduced drastically. Also, individual trees in some provenances have declined in vigor during recent years.

Despite these limitations, the overall performances of the surviving individuals in the majority of provenances have been consistent over the past 20 years. This is the only test of Douglas-fir in the central Great Plains and, thus, the sole source of data relating to the adaptability of Douglas-fir to this region. Therefore, it is deemed appropriate to report these data for their use in improving initial care and establishment procedures, and in the selection of seed sources in future tests.

Introduction

Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), the variety of primary concern in this study, occurs in most of the western mountain ranges east of the Coast Range in British Columbia and east of the Cascades and Sierra Nevada Ranges in the United States (Ryker and Steele 1980). Specifically, it is widely distributed in central British Columbia, southwestern Alberta, eastern Washington, Oregon, Idaho, Montana, Wyoming, southeast Arizona, and southern New Mexico; and locally in the mountains of northern and central Mexico (Little 1971, 1979) (fig. 1).

Coast Douglas-fir (*P. m.* var. *menziesii*), of which two provenances are represented in these data, occurs along the Pacific Coast eastward into the Cascade Mountains from southwestern British Columbia, through western Washington and western Oregon to central California; and in the Sierra Nevada to central California and western Nevada (Little 1971, 1979) (fig. 1).

Rocky Mountain Douglas-fir grows at elevations from 1,200 to 8,000 feet in the Northwest on a wide variety of soils and parent materials including granitic, volcanic, sedimentary, and metamorphic (Pfister et al. 1977). As Douglas-fir approaches its warm, dry limits (below 6,000 feet) towards the Great Plains, it becomes more restricted to basic soil parent materials such as andesite, basalt, and limestone (Ryker and Steele 1980); the latter type commonly occurs throughout the Great Plains region.

The plantation reported on here at 20 years of age, is part of a larger test of Douglas-fir provenances for which 1-year-old nursery and 3- to 8-year-old field data in Michigan and Nebraska plantations were reported (Wright et al. 1971). Eleven-year field performances of the provenances in this Nebraska plantation were reported by Read and Sprackling (1976). The objective of this study was to identify adapted sources of Douglas-fir for planting in the central Great Plains.

Materials and Methods

Seedling stock for the Nebraska plantation originated from 55 of 128 bulked sources of Douglas-fir seed assembled from native stands throughout the species range in the United States and Canada (Wright et al. 1971). The seeds were sown in an East Lansing, Mich., nursery in 1962; the seedlings were distributed to cooperators in 1963. The Nebraska seedlings were lined-out for 2 years before field-planting.

Small seedling size, a heavy-textured soil, and lack of protection from sun in the summer and protection from wind in the winter, in the Nebraska line-out beds, resulted in a 90% loss of seedlings over all provenances (97% within the Pacific Coast origins, 95% within the northern Rocky Mountain origins, and 71% within the central and southern Rocky Mountain origins) (Read and Sprackling 1976). Of the original 14 Pacific Coast provenances, only 22 seedlings of 6 provenances survived; of the 26 northern Rocky Mountain provenances, 56 seedlings of 19 sources survived; and of the 15 central and southern Rocky Mountain provenances, 187 seedlings of 13 provenances survived for field planting (Read and Sprackling 1976).

Surviving seedlings were field-planted in the spring of 1965 on a ridgetop of silt-loam, in single-tree, complete-

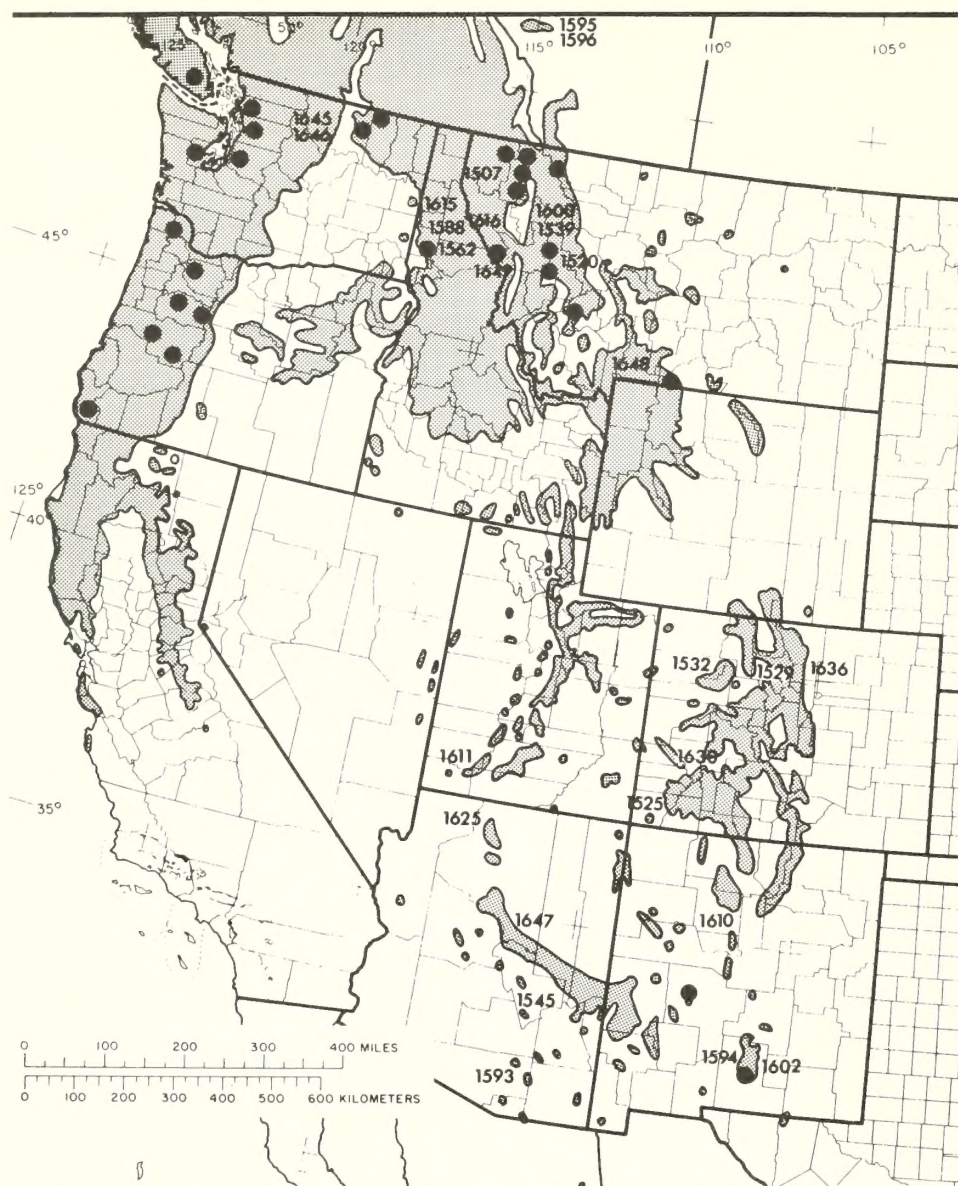


Figure 1.—Natural distribution of Douglas-fir, and provenances tested in eastern Nebraska. Numbers denote origins that survived; black circles, those that died in the nursery, or during first year after field planting (Read and Sprackling 1976).

ly randomized plots, spaced 12 feet apart in rows 12 feet apart. Unequal numbers of seedlings among the provenances precluded adherence to the intended randomized complete block design; thus, the seedlings were planted according to a completely randomized design. An eastern redcedar (*Juniperus virginiana* L.) seedling was planted between each Douglas-fir seedling, in the row, to provide early protection; they were removed in 1974 to avoid crowding.

Poor survival complicated the analysis of these 20-year data and, therefore, placed restrictions on any derived inferences. Several provenances were represented by a single tree and others by fewer than 10 trees, thus giving poor estimates of survival proportion. Additionally, several provenances had been replanted, and there was no within-plantation structure to the experimental design. Survival was not analyzed statistically in view of these limitations.

Analysis of variance ($P = 0.05$) and an unequal-sample-size multiple range test were applied to evaluate tree height growth. Significant variation was indicated among provenances; however, the multiple comparison test was sufficient to statistically detect only differences between the very tallest and the very shortest trees. Toward a goal of a more interpretable analysis, the provenance means were partitioned into groups with similar heights by a cluster analysis method (Scott and Knott 1974). Unlike a multiple range test that would identify pairwise differences in height growth among provenances, the cluster analysis method identifies group centers in a way that maximizes between-group variation (or equivalently, minimizes within-group variation). Similar to analysis of variance, significance of a particular partition of the provenances is assessed by comparing between-group vs. within-group estimates of variance with an adjustment of the latter to incorporate

the residual variance estimated in the initial analysis of variance. The data are clustered into successively larger numbers of groups until between- and within-group estimates of variance are not significantly different ($P=0.05$). The result is a nonsubjective partitioning of the provenances according to their height, which can be evaluated for geographic pattern. This analysis provides no information about differences between individual provenances, but it does assess the significance of differences between the centers of groups of provenances.

Phenotypic age/age correlations were computed at the tree and provenance levels for provenances with 3 or more trees of record and all provenances.

Results and Discussion

Survival

As Read and Sprackling reported (1976), in 1975, 11 years after field-planting, 77% of the seedlings of the 6 Pacific Coast provenances, and 61% of the seedlings of the 19 northern Rocky Mountain provenances had died. Only two Pacific Coast provenances (1645 and 1646) and 12 northern Rocky Mountain provenances had any survivors, with numbers per provenance ranging from 1 to 7 (table 1). No provenances from the central and southern Rocky Mountains were lost; but, mortality of seedlings averaged 37% and 11% in the central and southern provenances, respectively. Virtually all seedling mortality occurred during the first year in the field. Losses were attributed to heat and drought during the summer and to dessication of foliage in the winter on the relatively exposed ridgetop site.

In the 11-year analysis, Read and Sprackling (1976) clearly demonstrated the necessity of protecting Douglas-fir seedlings in the nursery and during early years in the field. They attributed the high mortality in the nursery to lack of shading and protection from wind during extremely hot and cold weather, and lack of moisture at critical times during the growing season.

Ryker and Potter (1970) demonstrated that shaded Douglas-fir seedlings survived more than twice as well (70% vs. 30%) as unshaded seedlings in field plantings. Shading reduces solarization, a process in which photosynthesis is inhibited by high light intensities (Ronco 1970).

In 1984, after 20 years in the field, numbers of trees per provenance ranged from 1 to 34, leaving 178 trees in 27 provenances (table 1). Only 1 tree, from provenance 1525 (s.w. Colo.), had succumbed during the 9-year period (1976–1984) following the 11-year evaluation. Surviving trees numbered 5, 22, 43, and 108 in the Pacific Coast, northern, central, and southern Rocky Mountain provenances, respectively (table 1).

These data indicate that, once established, Douglas-fir can survive in the eastern part of the central Great Plains to age 20; and that under the conditions of this test, the central and southern Rocky Mountain sources have survived best. There is indication, however, that some sources, especially those of southern origin, may not maintain this survival advantage. Observations in the

spring of 1986 revealed a decline in the vigor of some trees. Eight of 11 trees exhibiting decreased vigor (3 in 1532, and 1 each in 1526, 1611, 1625, 1545, and 1593) occurred in the southern portion of the species range. One tree each in the northern Rocky Mountain and Pacific Coast provenances 1588, 1596, and 1645 also showed a decline in vigor. Nonadaptability of individual genotypes to the matrix of environmental variables in the Great Plains probably explains this occurrence.

Height

Read and Sprackling (1976) reported that the seedlings, after becoming established in the field, grew at a mean annual rate of 1.4 feet from 1968 to 1975 (range 0.4 to 1.9 feet), and averaged 12.8 feet in height after 11 years (table 1). Variation in annual growth within the northern Rocky Mountain group was 33% (0.4 to 1.2 feet per year). Adaptive differentiation occurs in Douglas-fir across relatively small environmental gradients, of which there are many and steep (elevational) clines throughout northern Idaho, western Montana, and Canada. Thus, a moderately wide range of variation might be expected from within that region (Rehfeldt 1984).

Average tree heights among provenance groups (Read and Sprackling 1976) were tallest in the southern Rocky Mountain group (14.8 feet) and shortest in the northern Rocky Mountain group (6.9 feet) (table 1). Within the northern Rocky Mountain group average tree heights ranged from 3.4 to 10.1 feet. This pattern of taller growth in the southern provenances is reflected in the "percent of plantation mean" data, where percentages of 116 in the southern Rocky Mountain vs. 54 in the northern Rocky Mountain provenances were attained. Individual provenance means ranged from 140% in the Arizona provenance 1593 (Mt. Lemmon) to 27% in the Montana provenance 1648 (Big Timber) (table 1).

The relatively good height growth of the few surviving trees in the two Pacific Coast (central Washington) provenances, compared to the average height of trees in the northern Rocky Mountain provenances is of interest. The survival of these few provenance trees, originating from an arid sector of central Washington, seems explainable on a genetic basis. Douglas-fir populations characteristically possess a high degree of genetic diversity (Rehfeldt 1979, 1984). Given this diversity, any given generation produces some genotypes that are preadapted to environmental conditions outside the tolerance of the parental generation. Those individuals able to survive in the Nebraska environment, are most probably those individuals whose genetic constitutions can tolerate the extremes of the new (Nebraska) environment. The small number of trees surviving may be explained on the basis that the greater the distance from the source of origin, the smaller the number of preadapted genotypes capable of surviving in the new environment.

The clustering procedure (Scott and Knott 1974) used to analyze the 20-year results utilized height data from 14 of the 27 provenances, all of which had 3 or more surviving trees. Trees that had been replanted as seedlings

Table 1.—Twenty-year performances of surviving Douglas-fir trees of 27 provenances in an eastern Nebraska test.¹

Michigan State Univ. No.	Origin of Seeds		Latitude	Longitude	Elevation	Survival		Height		Plantation mean height				
	State or Provenance	Locale				Planted	Survived	11-year \bar{x} annual	20-year \bar{x} annual	1968-75	1975-86			
			°N	°W	ft.	no.		ft.		%				
Pacific Coast (var. <i>menziesii</i>)														
1645	WA	Fish Lake	48.6	119.7	2,000	7	4	4	10.4	1.1	22.8	1.2	81	93
1646	WA	Buck Mountain	48.4	119.8	5,000	5	1	1	8.9	1.1	22.0	1.3	70	90
					Subtotals and means	12	5	5	9.6	1.1	22.4	1.2	75.0	91.8
Northern Rocky Mountain (var. <i>glauca</i>)														
1615	ID	Coeur d'Alene	47.7	116.8	2,400	3	2	2	9.2	1.1	23.5	1.4	72	96
1588	ID	Wallace	47.5	116.0	3,000	9	7	7	8.8	1.0	22.3	1.4	69	91
1562	ID	Clarkia	47.0	116.1	4,500	5	2	2	4.5	0.5	17.5	1.3	35	72
1507	MT	Libby	48.4	115.5	3,800	1	1	1	9.8	1.2	24.0	1.4	77	98
1600	MT	Spotted Bear RS	48.0	113.0	3,680	1	1	1	6.4	0.8	20.0	1.4	50	82
1616	MT	St. Regis	47.5	115.2	4,000	4	3	3	10.1	1.2	22.3	1.2	79	91
1649	MT	Missoula	47.0	114.0	3,500	2	1	1	8.0	0.9	22.0	1.4	62	90
1520	MT	Greenough	46.9	113.4	4,000	4	1	1	9.5	1.1	26.0	1.6	74	107
1539	MT	Big Prairie RS	47.3	113.5	4,600	2	1	1	3.6	0.4	13.0	0.9	28	53
1595	AB	Kananaskia	51.0	115.0	4,500	2	1	1	5.7	0.7	19.0	1.3	45	78
1596	AB	Kananaskia	51.1	115.0	5,000	4	1	1	4.2	0.5	15.0	1.1	33	61
1648	MT	Big Timber	45.5	110.0	6,000	5	1	1	3.4	0.4	14.0	1.1	27	57
					Subtotals and means	32	22	22	6.9	0.8	19.9	1.3	53.9	81.6
Central Rocky Mountain (var. <i>glauca</i>)														
1636	CO	Boulder	40.2	105.5	8,650	14	7	7	8.6	1.0	21.3	1.3	67	87
1529	CO	Kremmling	40.0	106.5	8,000	5	2	2	9.0	1.0	22.0	1.3	70	90
1532	CO	Meeker	40.2	107.9	8,200	28	21	21	9.5	1.1	21.7	2.1	74	89
1630	CO	Ouray	38.2	107.6	9,100	3	1	1	11.4	1.3	27.0	1.6	89	111
1525	CO	Durango	37.5	107.8	8,500	12	8	7	12.7	1.4	24.6	1.2	99	101
1611	UT	Panguitch	37.6	112.5	8,250	5	5	5	9.7	1.4	20.6	1.1	76	84
					Subtotals and means	67	44	43	10.2	1.2	22.9	1.4	79.7	93.8
Southern Rocky Mountain (var. <i>glauca</i>)														
1610	NM	Jemez RD	35.5	106.8	8,500	29	28	28	14.9	1.6	26.0	1.1	116	107
1594	NM	Cloudcroft	33.0	105.8	8,670	11	8	8	15.1	1.7	27.0	1.2	118	111
1602	NM	Mayhill	32.9	105.4	7,000	37	34	34	15.7	1.7	26.8	1.1	123	110
1625	AZ	Fredonia	37.0	112.5	9,000	12	9	9	10.7	1.2	20.9	1.0	84	86
1647	AZ	Long Valley	34.7	111.0	7,000	12	12	12	14.0	1.5	25.0	1.1	109	102
1545	AZ	Globe	33.3	110.7	7,800	5	4	4	15.6	1.6	24.2	0.9	122	99
1593	AZ	Mt. Lemmon	32.4	110.8	8,400	14	13	13	17.9	1.9	28.5	1.1	140	117
					Subtotals and means	120	108	108	14.8	1.6	25.5	1.1	115.6	104.5
Plantation totals and means														
						236	178	177	12.8	1.4	24.4	1.2		

¹Extension of table in Read and Sprackling (1976).²Performance data above dashed line is less reliable because of limited number of trees.

did not materially influence the mean provenance heights in 1981 or 1984; thus, they were included in the analysis.

Two significantly different groups were identified in the analysis: a southern group (sources 1525, 1545, 1593, 1594, 1602, 1610, and 1647), with a mean height of 26.0 feet; and a mixed group (sources 1532, 1588, 1611, 1616, 1625, 1636, and 1645), with a mean height of 21.7 feet (fig. 2). Tree height, computed with provenance means, was significantly ($P=0.02$) and negatively correlated ($r=-0.61$) with latitude; correlation with elevation was weak ($r=0.21$). Subtle, but noticeable changes have occurred since the 11-year analysis when considering all provenance performances, regardless of numbers of surviving trees. Trees in provenances from the southern Rocky Mountains continue to be the tallest ($\bar{x} = 25.5$ feet), followed by central Rocky Mountain ($\bar{x} = 22.9$ feet), Pacific Coast ($\bar{x} = 22.4$ feet), and northern Rocky Mountain ($\bar{x} = 19.9$ feet) provenances. However, 9 years later, there is a change in the relative values of mean annual growth. Trees in the southern Rocky Mountain provenances have decreased in mean annual growth from 1.6 to 1.1 feet, but trees in the northern Rocky Mountain provenances have increased from 0.8 to 1.3 feet per year. The rankings among provenance groups for "percent of plantation mean" have remained the same, but the 1975 vs. 1984 percent of plantation mean values show gains in 1984 of +27.7%, +16.8%, +12.1%, and -11.1% for the northern Rocky Mountain, Pacific Coast, central Rocky Mountain, and southern Rocky Mountain provenances, respectively (table 1). The relative improvement in height growth of the northern provenances over the southern sources is slight but discernible (fig. 3).

The decline in rate of height growth in the southernmost provenances is apparently due to periodic dieback of terminal growth caused by periodic winter injury.

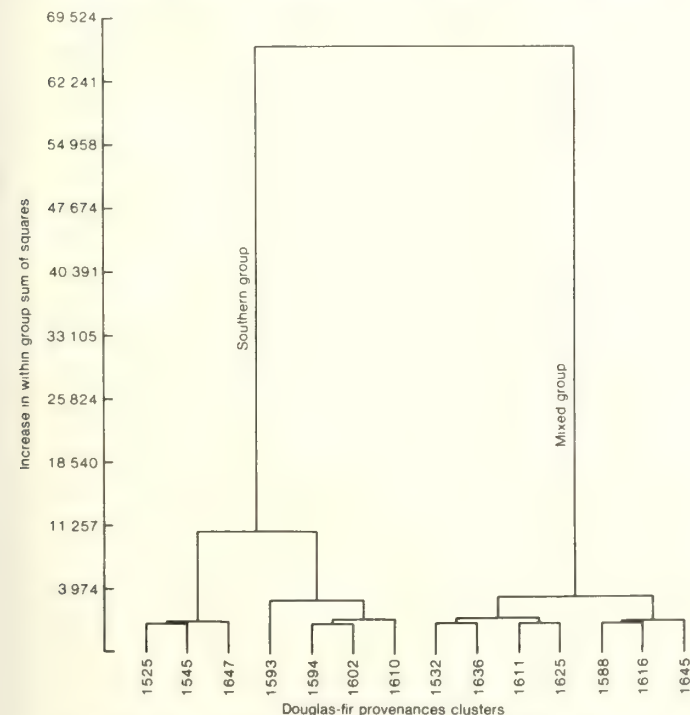


Figure 2.—Height clustering of Douglas-fir provenances

Trees in provenances 1545 (Globe, Ariz.) and 1647 (Long Valley, Ariz.) incurred terminal damage from freezing in 1969, 1971, and in 1981–1984 (fig. 3). The decline in vigor of trees in the central (1525, 1532, and 1611) and southern provenances (1545, 1593, and 1625) may have contributed to the decline in relative height growths. Thus, there appears to be a slight, but perceptible, pattern of increased height growth of the northern provenances relative to southern provenances.

Winter Injury

Winter injury, expressed by the amount of terminal dieback, was evaluated in the present evaluation at age 12 (winter 1976–77). Injury was detected on 1 of 5 surviving trees in the 2 Pacific Coast provenances, and on 1 of 22 surviving trees in the 12 northern Rocky Mountain provenances (table 2). Sixty-seven percent of the trees in the southern Rocky Mountain provenances suffered some terminal dieback, ranging from 49% in the Fredonia, Ariz. provenance (1625) to 100% in the Globe, Ariz. (1545) provenance (table 2). Less injury (16%) occurred in the 6 central Rocky Mountain provenances.

The pattern of injury was consistent with that reported by Read and Sprackling (1976); they found that injury within provenances occurred on the same trees in successive years. Winter injury had not caused the death of any trees; the killed terminals were replaced by one or more lateral branches, one of which assumed dominance (Edgren 1970). Despite repeated dieback of terminals on some trees within the southern provenances, growth each year exceeded the loss of terminal growth occurring at irregular intervals. Exceptions may be the Arizona provenances 1545 and 1647, which appear in doubt of maintaining the growth/loss ratio (fig. 3). Northern provenance trees incur very little winter injury; their shorter heights has been attributed to later initiation of the growth processes in the spring and earlier cessation of the process in the fall (Wright et al. 1971, Campbell and Sorenson 1973).

Susceptibility of the same trees within provenances to incur repeated terminal dieback can be attributed to genetic variability among trees within a provenance locale. The genotypes of such trees, due to adaptive differentiation within provenance microsites, are variable within local populations in their tolerance to the extremes of variation in environmental factors present at the test site (Van Haverbeke 1968, Rehfeldt 1984).

The higher percentages of seedling loss in the nursery among provenances of northern origins compared to lower losses of seedlings among southern origins, seems a contradiction to the relatively higher percentages of winter injury in the field among seedlings of southern origin reported by Read and Sprackling (1976). The relatively smaller size and, thus, perhaps physiologically weaker condition of the northern seedlings while in the nursery, may account for this initial loss.

Age/Age Correlations

Height at age 20 was poorly predicted in all but the most recent measurements when computed at the tree

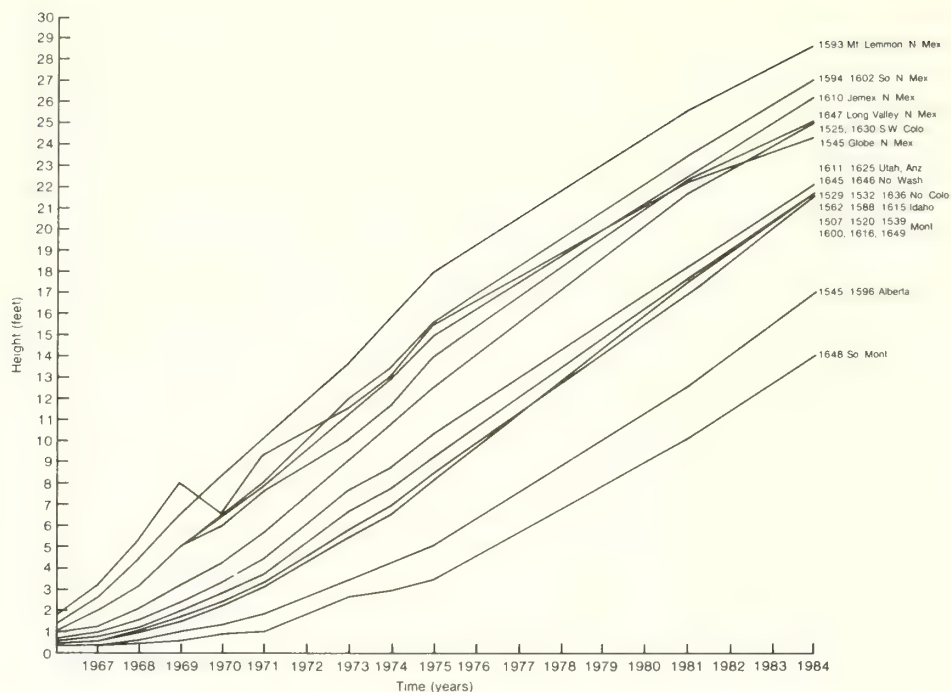


Figure 3.—Height growth curves for Douglas-fir origins (some grouped) after 20 years in an eastern Nebraska plantation (extension of fig. 2, Read and Sprackling 1976).

Table 2.—Winter injury (terminal dieback) in Douglas-fir provenances, winter 1976–77.

Mich. State Univ. Prov. No.	Location	Trees surviving in 1977	Trees damaged	Trees damaged	\bar{x} damage per tree
		no.	no.	%	ft.
Pacific Coast					
1645	WA	4	1	25	2.0
1646	WA	1	0		
Northern Rocky Mountain					
1615	ID	2	0		
1588	ID	7	1		
1562	ID	2	0		
1507	MT	1	0		
1600	MT	1	0		
1616	MT	3	0		
1649	MT	1	0		
1520	MT	1	0		
1539	MT	1	0		
1595	ALB	1	0		
1596	ALB	1	0		
1648	MT	1	0		
Central Rocky Mountain					
1636	CO	7	0		
1529	CO	2	1	50	1.0
1532	CO	21	4	21	1.0
1630	CO	1	0		
1525	CO	8	1	12	1.0
1611	UT	5	1	20	3.0
Southern Rocky Mountain					
1610	NM	28	20	71	2.0
1594	NM	8	5	62	1.4
1602	NM	34	23	68	1.9
1625	AZ	9	4	49	1.0
1647	AZ	12	7	58	2.4
1545	AZ	4	4	100	4.0
1593	AZ	13	9	69	2.4
Total		178	81		
\bar{x}				46	2.2

level. However, phenotypic age/age correlations computed at the provenance level, where the mean was adequately described with 3 or more trees, showed steadily improving values with decreasing time intervals; the indication was that mean provenance height could be adequately predicted at age 6 (1970) (table 3).

Conclusions and Recommendations

Twenty-year performance results are in close accord with those reported at age 11 by Read and Sprackling (1976). Survival data suggest that, in eastern Nebraska, Douglas-fir seedlings will incur heavy mortality in the nursery and during early years in the field unless seedlings are of good quality and are protected from solarization, drought, and winter exposure. These results indicate that well-developed planting stock is necessary to insure field survival; stock of 2 + 1 or 2 + 2 age class, possessing a well-balanced shoot-root ratio, should be planted. Protection can be provided by sheltering seedlings in lath- or shadehouses prior to field planting; and

by shielding seedlings individually with "cedar shingles," or by interplanting a faster growing, but temporary "nurse" tree species such as eastern redcedar (*Juniperus virginiana* L.). Avoidance of frost pockets and exposed sites is also advised.

This study found that trees of southern Rocky Mountain origin survive better and are taller after 20 years than trees of most central Rocky Mountain and northern origins. Once established, however, the surviving trees of northern sources persist and, because of lack of winter injury, appear to be slowly narrowing the height advantage gained earlier by the trees of southern sources. Central Rocky Mountain sources are relatively winter hardy and grow quite well; they are recommended for ornamental planting in the eastern part of the central Great Plains. They also may be suitable for establishing windbreaks around farmsteads and in urban plantings where protection and water can be provided. As in the 11-year evaluation, the southwest Colorado provenances 1525 (Durango), and especially the high-elevation provenance 1630 (Ouray), because of its trees of good vigor, continue to be recommended.

Table 3.—Phenotypic age/age correlations computed at the provenance level among ages 2 to 20 for 14 provenances of Douglas-fir.

		Correlations										
Age -----	2	3	4	5	6	8	9	10	11	17	20	
Year -	1966	1967	1968	1969	1970	1972	1973	1974	1975	1981	1984	
2		.99	.98	.98	.89	.92	.86	.84	.86	.81	.68	
1966												
	3		1.00	.99	.91	.94	.88	.86	.88	.84	.71	
	1967											
		4		1.00	.94	.96	.91	.89	.91	.87	.75	
		1968										
			5		.94	.96	.91	.89	.91	.87	.75	
			1969									
				6		.99	.99	.98	.99	.98	.91	
				1970								
					8		.98	.98	.99	.97	.88	
					1972							
						9		1.00	1.00	.98	.93	
						1973						
							10		1.00	.98	.94	
							1974					
								11		.98	.93	
								1975				
									17		.95	
									1981			
										20		
										1984		
Age		Year		Prov.		\bar{x} height		SD				
				no.		ft.						
2		1966		14		0.92		0.37				
3		1967		14		1.44		0.76				
4		1968		14		2.41		1.31				
5		1969		14		3.70		1.97				
6		1970		14		4.63		1.93				
8		1972		14		5.92		2.35				
9		1973		14		9.00		2.54				
10		1974		14		10.38		2.82				
11		1975		14		12.25		3.13				
17		1981		14		20.04		2.94				
20		1984		14		23.87		2.54				

The southern Rocky Mountain provenances incur the most winter injury. However, they recover and are the fastest growing provenances as a group. If adequately protected, provenances 1593 (Mt. Lemmon, Ariz.), 1594 (Cloudcroft, N. Mex.), and 1602 (Mayhill, N. Mex.) are recommended, with caution, for Christmas trees, where short rotations decrease the probability of severe loss during the occasional winter of unusually cold temperatures. The foliage of trees from Arizona and New Mexico also is uniformly among the bluest (Wright et al. 1971)—a desirable Christmas tree characteristic.

In view of the appreciable gain in percent-of-plantation mean (+27.7), (table 1) of the northern Rocky Mountain provenances during the past 9 years, this region should not be overlooked as a source of material of high potential for the central Great Plains. Trees of northern Idaho (1588 and 1615) and western Montana (1507, 1520, and 1616) provenances, although few in number, performed well in this test. They may ultimately prove superior to the above-recommended central and southern Rocky Mountain provenances in terms of survival and height growth. Further testing of Douglas-fir is recommended—appreciating the limitations of funding, the availability of material, and the time required to obtain definitive results. An alternative, assuming adequate seed production, would be to remove the undesirable phenotypes and provenances in the present test and allow the remaining trees to interbreed. Performances of the original provenances would serve as controls. Phenotypic age/age correlations indicated that provenances expressing superior height growth can be identified by age 6.

It is appreciated that the number of provenances and the number of surviving trees in many of the provenances is small—especially in the northernmost provenances. However, the performance patterns among individual trees, provenances, and groups of provenances during the past 20 years has been impressively consistent.

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Van Haverbeke, David F. 1987. Genetic variation in Douglas-fir: A 20-year test of provenances in eastern Nebraska. USDA Forest Service General Technical Report RM-141, 8 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Twenty-year-old Douglas-fir trees from Arizona, New Mexico, and southern Colorado survived better, grew taller, but incurred more winter injury in eastern Nebraska than trees from northern provenances. Northern trees increased in percent of plantation mean height in past 9 years. Provenances expressing superior height are identifiable at age 6.

Keywords: *Pseudotsuga menziesii* var. *glauca*, *P. menziessii*, provenance, seed source, age/age correlation, winter injury

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Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

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Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota
Tempe, Arizona

* Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526

081 RM-142
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Forest Service

Rocky Mountain
Forest and Range
Experiment Station

Fort Collins,
Colorado 80526

General Technical
Report RM-142



Biology and Conservation of Northern Forest Owls

Symposium Proceedings

February 3 - 7, 1987
Winnipeg, Manitoba

Nero, Robert W.; Clark, Richard J.; Knapton, Richard J.; Hamre, R. H., eds.
1987. Biology and conservation of northern forest owls: symposium proceedings.
1987 Feb. 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO:
U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and
Range Experiment Station; 309 p.

Proceedings of this first international symposium consist of 47 presented papers covering 15 owl species, and 4 workshops dealing with capture, telemetry, census, and management techniques. Basic information on habitat preferences, home range size, detecting lesser known owls, etc. will be invaluable to managers of wildlife and of forested lands; techniques information will be invaluable to researchers.

SUPPORTERS:

Air Canada
Canadian Nature Federation
City of Winnipeg
Manitoba Naturalists Society
Manitoba Wildlife Federation
Richardson Century Fund
Saskatchewan Natural History Society

EXHIBITORS:

Hazel Birt, James Carson, Audrey Casey,
Carole Dempster, Roy Erskine, Tim Garton,
Paul Guyot, Dennis Hillman, William McCracken,
Terry McLean, Glen Moncrieff, Heather North,
Lynn Ohryn, Norm Peterson, Bob Pollock,
Jim Russell, Peter Sawatsky, Roy Simmons,
Robert R. Taylor, and Clarence Tillenius.

COVER:

A Great Gray Owl drops in for
dinner near Helsinki, Finland.
Photo by Seppo Niiranen.

Biology and Conservation of Northern Forest Owls

Symposium Proceedings

**February 3 - 7, 1987
Winnipeg, Manitoba**

Editors:

**Robert W. Nero, Manitoba Department of Natural Resources
Richard J. Clark, York College of Pennsylvania
Richard J. Knapton, University of Manitoba
R. H. Hamre, Rocky Mountain Forest & Range Experiment Station**

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Preface

IN 1983, Bob Nero began to talk about the need for a gathering of "owlologists" to compare notes on Great Gray Owl research and conservation. At that time, he contacted a few colleagues who also expressed a great need to review their work and exchange ideas on research techniques. Little did any of us realize at the time that the need was international, that the forum would be 3 1/2 days of technical presentations and workshops, and that "owlologists" would be discussing all northern forest owl species at the first-of-its-kind Symposium held in Winnipeg, Manitoba, Canada, February 3-7, 1987.

The timing was right on. The organizers worked hard. Sponsors' interest was high. Eventually a program was developed that included a field trip, exhibits, musical and social events, all planned to provide a restful change from intense discussions and to effect international camaraderie. It worked. How well it worked can only be known from those who were there!

As the coordinating chairman for the Symposium, I had the pleasure of working with a central committee composed of Bill Koonz (Arrangements), Bob Nero (Program) and Ken De Smet (Finances). Excellent support for this committee came from office staff, university professors, volunteers, students and biologists. They are: Lori Bartley, Lynn Bergeron, Don Campbell, Brendan Carruthers, Maureen Collins, Herb Copland, Dr. Jon Gerrard, Chris Hofer, Kathryn Johnston, Rudolf Koes, Dr. Erkki Korpimäki, Dr. Emil Kucera, John Morgan, Ted Muir, Dr. Ronald Ryder, Ulrike Schneider, Renate Scriven, Dr. Spencer Sealy, Don Sexton, Dan Soprovich, Linda Tardiff, Rick Wishart and Rosemarie Young.

The production of a printed Proceedings was accomplished in record fashion due to the outstanding cooperation of the many contributors who submitted camera-ready manuscripts and illustrations. Bob Hamre is obviously a seasoned

veteran in producing a quality publication. He was aptly assisted by the editorial committee consisting of Bob Nero, Dick Clark and Richard Knapton. Only the authors are responsible for the material contained in their papers; their views are not necessarily those of the sponsors, i.e., the USDA Forest Service, the Wildlife Society, World Wildlife Fund, University of Manitoba, and the Manitoba Department of Natural Resources.

How have northern forest owls benefitted from this Symposium? There was an initial, very positive response from the public and local news media to the holding of such an event. However, the full effect of this meeting will not be realized until the technical knowledge exchanged during the Symposium and recorded in this document is incorporated into action programs by management agencies and pushed by conservation groups. This challenge was presented by Monte Hummel in his opening address and recognized by Dick Clark in his summary remarks.

Canada celebrates 100 years in wildlife conservation in 1987 under the theme Wildlife '87: Gaining Momentum. During a time when nongame wildlife programs are fledging and taking wing in Canada, it is appropriate that we would begin the second 100 years with a Northern Forest Owl Symposium as the first event of this celebration. By the time the next Northern Forest Owl Symposium is held, I hope that action programs will have been implemented to protect owls where needed and to ensure that the public will have a greater understanding and appreciation of the role of owls in the natural environment.

Merlin W. Shoesmith,
Chief, Biological Services,
Wildlife Branch,
Department of Natural Resources,
Winnipeg, Manitoba.

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Official Opening Remarks'

Leonard E. Harapiak²

Mr. Chairman, distinguished guests, owl biologists, ladies and gentlemen. On behalf of Premier Pawley and the Province of Manitoba, I will officially open the Northern Forest Owl Symposium. To those visiting delegates from northern Europe, the United States, and other Canadian provinces and territories: welcome to Manitoba! Your presence here has ensured that this meeting will be a success. I am advised that some of you have gone to considerable effort to get here. I hope that your brief stay in Winnipeg and participation in this conference will be very enjoyable and will bring you back soon.

I would also like to congratulate the organizers of this event. I am sure that their hard work in developing the program and making all the arrangements will be evident during the next four days. I understand that the auction being held later this evening features contributions by Manitoba wildlife artists, many of them exhibiting their work during the symposium. Thank you to all contributors; the proceeds will go to support the symposium and to owl conservation.

1986 was and 1987 will be special years for wildlife conservation in Canada. Last year, the World Wildlife Fund, a network of 23 national organizations working to maintain the biological resources of the earth, celebrated its 25th anniversary. The Canadian affiliate has been a particularly good friend to wildlife in Manitoba, and I intend to speak more directly on that later this evening.

The Canadian Wildlife Federation also celebrated its 25th year in providing support for the protection of natural resources in Canada. Coincidentally, 1986 was the 25th anniversary of Manitoba's Wildlife Management Area Program. Over 7 million acres in 59 areas have been designated for the management of wildlife and public use of the resource. Many of them greatly assist in conserving owls.

During 1987, Canada will celebrate 100 years of wildlife conservation. As an initiative by the Canadian Nature Federation, a number of major events

will occur under the theme "Wildlife '87: Gaining Momentum". They include:

- the Northern Forest Owl Symposium
- International CIES conference in Ottawa July 12-24th
- Last Mountain Lake dedication ceremonies with Prince Philip in Saskatchewan

I am very pleased that Manitoba will be the first to celebrate 100 years of conservation in Canada by focusing attention on owls of the boreal forest. This is the first symposium of its kind to be held anywhere in the world. It is my hope that it will not be the last. It should become a regular event to bring together the best collective biological wisdom on forest owls and to provide decision makers with the basis to make sound decisions to conserve populations of these magnificent birds.

One of these magnificent birds is with us tonight. Lady Gray'l, a Great Gray Owl, has been maintained in captivity by Dr. Robert Nero of my staff for use in public education and research for the last 2½ years. She has visited many school rooms and shopping malls and has captured the hearts of many Manitobans.

While southeastern Manitoba has a substantial population of these owls, it is still declared a rare species across Canada. Manitobans have a special obligation to ensure that Great Gray Owls persist in Canada and to afford protection to other owl species in jeopardy.

Because of the symbolic nature of Lady Gray'l, I expect that the Great Gray Owl will be officially designated as Manitoba's provincial bird during the forthcoming session of the Manitoba Legislature.

In order to ensure that Great Gray Owls as well as all wildlife species will receive the necessary resources required to manage and protect them, I have asked my staff to prepare a non-game plan. This plan will ensure efficient use of available funds, staff, student and volunteer time. I will as well need the help of many of you and others as leaders of conservation organizations here tonight to co-operatively support its implementation.

In closing, I would like to express my gratitude to the co-sponsors and contributors who have come forward with their generous support that will make this symposium a success. It is with great personal pleasure that I now declare the Northern Forest Owl Symposium to be officially open.

¹Presented at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

²Minister, Manitoba Department of Natural Resources.

Owls: Who Gives a Hoot?¹

Monte Hummel²

Owls mean something to me. They've kept me company, lulled me to sleep and just generally made life more worth living. I'm sure the same is true for everyone else in this room. Yet, what thanks have people extended to owls for their companionship and for their very important role in nature?

Well, on a world-wide basis IUCN already lists 13 species of owls in the Red Data Book. I'm always interested to hear my colleague Jen's Wahlstedt from Sweden telling me exactly how many pairs of Eagle Owls they have and where each one is.

Here in Canada, of course, we've managed to put one owl species on each of our endangered, threatened and rare lists - the Spotted Owl, Burrowing Owl and Great Gray Owl respectively. We've cut the old growth timber habitat of the Spotted Owl in B.C. We've plowed up, shot and likely poisoned the Burrowing Owl in Alberta, Saskatchewan and Manitoba. And, although it has always been found in relatively low numbers, we're making sure the Great Gray Owl stays that way by cutting down some of its critical Tamarack nesting areas right here in Manitoba.

If you combine the IUCN world assessment to date, add the Canada lists with other similar national inventories, throw in a little common sense, and I think an intelligent guess would be that up to 20% of the world's 133 owl species have been either endangered or seriously jeopardized by the activities of people.

Makes you think doesn't it?

It makes me think. I makes me wonder whether the creator didn't put these birds on the planet to hoot out a question (if you'll pardon the pun), "Just who who the hell do you humans think you are?"

Well, who indeed do we think we are? Who are we, one species, to have assumed control of the earth's evolutionary fate, responsible for the extinction of other species at an unprecedented level? Who are we to cause extinctions, conservatively speaking, at the rate of three per day, by the late eighties one per hour, and by the turn of the century up to one million species either endangered or extinct? Who are we to have unleashed a rate of extinction 400 times greater than anything experienced in recent geological time? And who are we to have been responsible for all this, but to have refused responsibility for it?

Perhaps the numbers and estimates I gave earlier regarding owls don't really indicate that owls as a species-group are in any greater risk than any other. Rather, and this may be the most important conclusion, owls are quite representative of a trend being experienced by all forms of wildlife.

The organization I represent, World Wildlife Fund, is best known for trying to do something about rescuing species from extinction, or "preserving genetic diversity" as it is stated more grandly in the World Conservation Strategy. Since our founding in 1961, WWF has raised over \$200 million for 5,000 projects in 130 countries.

Peanuts, that amount of money wouldn't even buy you five F-18 Jet Fighters, and Canada just ordered 138.

Some enterprising journalist recently identified 100 species saved as a direct result of WWF's efforts.

Peanuts again, when you consider we'll be losing 100 per day within a matter of years.

So what can we do that amounts to anything? Simply stated, but it's difficult to do, if we seriously want to stem the tide of human-caused extinctions, we must focus our efforts on conserving biological systems. Save a system and you save the components. The cold fact is that we are losing entire systems - for example the tropical forest and wetlands on an international scale, for example the prairie grasslands the Carolinian Zone, and wetlands here in Canada.

Of course this is precisely why WWF Canada last year opened an office in Calgary and launched our three-year Wild West program which has

¹Opening address presented at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM 142.

²President, World Wildlife Fund Canada.

already funded over 30 projects involving 40 different conservation groups and agencies from western Canada. We are also drafting a Prairie Conservation Action Plan which will serve as a blueprint for action on the remaining tallgrass, mixed grass, shortgrass and aspen parkland prairie eco-systems - all of them more than 80% lost to cultivation or grazing. This work is being done in co-operation with ranchers, farmers and other land owners to encourage private stewardship and conservation farming techniques. Since native grasslands are the most endangered wildlife habitats in Canada, WWF has taken the further step of inviting our International President, Prince Philip, to visit western Canada in this 100th year of wildlife conservation, to publicize the international significance of western Canada's conservation concerns. All of this is pursuing that principle I mentioned earlier: "Save a system and you save the components." In this case, save the prairies and you save about half the birds and mammals classified as endangered so far in Canada.

To be sure, there are species-related steps that can be taken. Getting back to our owls, for example, WWF has supported conservation work on all three species listed by the Committee on the Status of Endangered Wildlife in Canada.

For the endangered Spotted Owl, we are supporting a captive breeding program at the Owl Rehabilitation Research Foundation with an eye to reintroductions in this country.

For the threatened Burrowing Owl, we have supported the first banding programs in all three prairie provinces. We are working co-operatively with landowners to protect pastures where nesting

burrows are found. We are helping pioneer artificial underground nesting boxes, and we are assisting with the drafting of a national recovery plan.

For the Great Gray Owl, we have supported work in Ontario into the question of why these birds invade the southern part of that province during winter, and we have supported Bob Nero's work on radio telemetry and protection of the nesting habitat in southeastern Manitoba.

However, there is one more thing you could do, and I want to close by proposing it this evening.

WWF Canada is already assisting with the publication costs of the proceedings of this symposium, and I am sure these will serve as a useful update on the behavior, ecology and physiology of North America's owls for researchers everywhere. But really, all the outside world wants to know is what overall trend do these more technical papers indicate? Therefore could we not take an additional step with a statement of concern, perhaps similar to the wolf manifesto produced by IUCN's specialist group on that species? Specifically, I'm proposing that a message be sent out at the closing of this meeting that says, hey, our beast is appearing on these bloody endangered species lists! We are concerned and we are speaking up. Because what is happening to owls is sadly representative of what's happening to wildlife in general. And we find this situation just plain unacceptable. It cannot and must not continue.

Who gives a hoot about owls? We do! Now it's time to let a few more people know about it.

Symposium Summary and Concluding Remarks¹

Richard J. Clark²

Abstract.--To summarize the geographic location of the researchers: of the 150 registrants, 22 (15%) were from eight European countries (Norway, Finland, and Sweden topped the list), 83 (53%) were from five Canadian provinces and one Territory, and 45 (30%) were from 17 States of the United States. Of the 52 papers presented, 39 dealt with research on a single species, four dealt with two species, and seven dealt with more than two species. Of those, three dealt with community studies of owls. Eighteen papers dealt with aspects of the basic behavior of species and 12 papers dealt with the habitat of owl species in some detail. The conference brought from obscurity some of the basic biology of *Otus flammeolus*, the Flammulated Screech Owl, and its distribution on the periphery of its range in British Columbia, and the latter can also be said about the population of Spotted Owls, *Strix occidentalis*, in that same province. Much basic information that will be invaluable to land and wildlife managers -- such as habitat preference, home range size, detecting lesser known owls, etc. -- was presented.

SUMMARY AND CONCLUDING REMARKS

Someone has said that to summarize a conference such as this has been, is an impossible task but I would like to thank Dr. Robert Nero for providing the opportunity to try. I would also like to thank, on behalf of the participants if I might be so presumptuous, Dr. Merlin Shoesmith and all of the other Manitobans for the splendid job they have done in organizing and executing this Symposium. Having lived in Manitoba for a couple of summers I found the people of this province to be memorably hospitable and this trip has reinforced that feeling of warmth in spite of the outside temperatures.

¹Concluding address at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

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I shall start out by admitting up front that I was unable to hear all of the papers presented. That arises from the fact that on Tuesday evening I was conducting an auto census of the owls of the forests of northern Minnesota, eastern North Dakota, and southern Manitoba. I selected a strip transect to sample the area and the strip consisted of a band starting at the Minneapolis/St. Paul Airport and ending at the Viscount Gort Hotel in Winnipeg, Manitoba, Canada. I choose 100 meters from the center of the motor car route on either side of routes 494, 94, and 49 as the specific sampling area. The dimensions of the sampling plot are actually 300 kilometers by 200 meters. Admittedly only the shelterbelts and riparian woodland were suitable habitat and I must subtract 12 kilometers of the strip where dense fog, associated with sugar beet refineries, prevented my seeing any owls. Unfortunately I did not see a single owl within the study area. The only good aspect of that fact is I do not have to ponder which statistic is most appropriate to apply to my results. All of this is offered as the reason underlying my sleeping Wednesday morning when I should have been listening to papers.

Secondly, I would like to define some of the technical terms that have been used at the conference for the benefit of those readers of the proceedings. Some of these terms are similar to terms used in everyday language, but they have special meaning here, thus I shall gloss them. I shall take the terms in alphabetical order. The first term is Bastard and this has to do with mixed ancestry. Now this was not the actual term used by the presenter and when I talked with him about my using the term he suggested that it perhaps had a negative connotation. So to avoid that possibility I shall use that term Complication. We saw how Strix aluco and Strix uralensis were equally implicated in complicating the ancestry of certain generations in Bavaria. Next we have Divorce which is used to refer to the dissolution of pair bonding between mates. This was used to define bonding between individuals of the same two species earlier mentioned. Then we have Secondary Females. In the human condition this might be thought of as being analogous to playing second violin in an orchestra. We saw how "playing second fiddle" has inherent risks within Surnia ulula populations. Finally we have the term Topless and when applied to the human condition this may mean that the upper portion of the torso is unadorned of garments or is naked. Here specifically it refers to the torso of a nest cavity box being naked of a roof. Enough of that--let me now try to be serious for a few minutes.

First allow me to summarize the geographic location of the researchers. This information was taken from the official list of registrants. I have deviated from that list only insofar as I have recorded Dr. Heimo Mikkola as a resident of Finland rather than Indonesia as suggested by the list. I will play the numbers game for just a moment by saying that of the 150 registrants 22 (15%) were from eight European countries, 83 (53%) were from five Canadian provinces and one Territory and 45 (30%) were from 17 states of the United States. Norway, Finland and Sweden topped the list for numbers of participants from Europe and not surprisingly Manitoba and Saskatchewan provided the largest numbers from Canada while Minnesota, Wisconsin, Colorado and Oregon were the home states providing the largest numbers from the United States.

This says nothing about the quality of the presentations which were overall splendid from all countries. It was especially heartening to hear from Spain, Hungary, Czechoslovakia, and the USSR

even though our colleagues from the latter three countries were unable to travel to the symposium. I trust the readers are aware of the solid contributions from Scandinavia and West Germany and my comments citing specifically representation from these countries will not offend those from other countries. While humans recognize political borders, owls do not; hence, it is important to hear from researchers from all geographic locales within owl species distributional ranges.

I will now shift my emphasis to where it most appropriately belongs--to the owls themselves. I have, from the abstracts, compiled the following data [see Table 1] on a species by species basis and would caution that this compilation was done while watching slides and listening to presenters, hence must be considered a preliminary to the final report that will appear in the Proceedings. For emphasis, I will start by pointing out that seven of the 22 species targeted (perhaps a bad choice of words) selected to be the subject of this conference were not reported on at all. It is not at all surprising that five of the seven are species of Otus for 32 of the 136 species of owls commonly recognized are of the Genus Otus. They are, to enumerate, Otus kennicotti the Western Screech-Owl, Otus bakkamoena the Collared Scops-Owl of Asia, Otus brucei the Striated Scops-Owl [also of Asia] Otus scops the Common Scops-Owl of Africa, Eurasia and Indonesia and Otus sunia the Oriental Scops-Owl. In addition, we have heard nothing about Blakiston's Fish Owl Ketupa blakistoni of Japan and Korea nor Ninox scutulata the Oriental Hawk Owl which is widespread in Asia and Indonesia. Lest one think I am totally negative I would hasten to add that this conference has brought from obscurity some of the basic biology of Otus flammeolus the Flammulated Screech Owl, and its distribution on the periphery of its range in British Columbia and the same can be said about the population of Spotted Owls Strix occidentalis in that same province. Eighteen papers dealt with aspects of the basic behavior of species and we saw how techniques of hybridization, which can be an essential tool for isolating details on the genetic component of species-specific behaviors can be utilized with owl species. Food habits are always going to be an important aspect of predator studies; however they have reached the point where they are now well enough known on some species that they are now a means to the end of elucidating ecological relationships rather than being an end in themselves. Twelve

Table 1.--Summary of symposium papers; subject species, topic(s) and geographic location(s).

	ANATOMY	DISTRIBUTION	BASIC BEHAVIOR	FOOD HABITS	HABITAT	NESTING BIOLOGY	POPULATIONS	RADIO-TELEMETRY USED	TAPE-PLAYBACK USED	TOTAL NO. OF STUDIES REPORTING	GEOGRAPHIC LOCATION
Flammulated Owl ¹		1	2		1	1	1			4	BrC, Co
Eastern Screech-Owl		1	2	1	2		1	1	4	5	MI, CT, Sas
Western Screech-Owl										1	Literature Mentioned
Common Scops-Owl										1	Literature Mentioned
Striated Scops-Owl										1	Literature Mentioned
Oriental Scops-Owl										1	Literature Mentioned
Collared Scops-Owl										1	Literature Mentioned
European Eagle-Owl				1				1		3	Norwa, Spain
Great Horned Owl	3				1	1	1			7	Alb, MI, MT, Sas
Blakiston's Fish Owl										1	Literature Mentioned
Northern Hawk-Owl	2		4	1	1	4		1		8	Alb, Finla, Norwa (2), Ont, Sas
Northern Pygmy-Owl	1									2	Alb
Eurasian Pygmy-Owl			1	1					1	3	Norwa, Swede
Oriental Hawk Owl										1	Literature Mentioned
Barred Owl	2		1		5	2		2	1	9	MI, MN (2), NJ, Sas, WA
Spotted Owl		1	2		1	2		2	1	3	BrC, OR, WA
Great Gray Owl	2	2	1	5	7	4	2	3		12	AK, CA, Finla (2), Man(3), MI, MN, OR, Sas
Tawny Owl			1	3	2	1				4	Finla, Germa(W), Spain
Ural Owl			2	1	1	1		1		3	Finla, Germa(W)
Long-eared Owl	3		1							5	MN, USSRu
Boreal or Tengmalm's Owl	4	3	5	1	5	3	1	2	1	14	CO(2), Finla, MT, Norwa, Sas, Swede, WA, WI
Northern Saw-Whet Owl	3		2	2	4	1	1	1	1	9	Alb, BrC, CO, MI, MN, MT, Sas, WI

¹ See Northern Forest Owl subject species list for scientific binomials.

Location Legend: the following "abbreviation" scheme was used for reporting the location for each respective study--Canada [a three letter abbreviation for the Province or Territory], International [a five letter abbreviation for the country], United States [the standard two letter U.S. postal abbreviation].

papers dealt with the habitat of owl species in some detail and hopefully this area of research will expand from here, for a suitable place to live is no doubt even more critical to the survival of owl species than it is to man. I did not tally man-owl aspects and they were not here emphasized, however, we did see that there are some areas that are the cause for concern particularly with regard to species of Bubo. With regard to Bubo there is some good news and some bad. The good news is that through the dedicated efforts of an individual and his wife a cadre of volunteers was developed which changed the image of the Great Horned Owl in central Canada, while in Europe man continues to be a threat to the survival of the Eagle Owl, either directly through his activities or indirectly through his anthropogenic structures. The basic biology of nesting and population dynamics have been reported but there is certainly room for more research in these areas. The latter aspect is particularly crucial if we are to insure the survival of existing species that are rare, threatened or endangered and also if we are to manage species that are common, in a manner that will minimize conflict with man in relations with those species.

I will now turn to some broader aspects of the research that has been reported here as well as some points that have been made in discussion. I view **basic research, applied research, and conservation** as seen in this triangle [Figure 1]. You will note that I have represented basic research as the foundation for this triangle, i.e., it must necessarily form the basis for sound applied research and/or effective conservation and management of owl species. As one can see in the triangle basic research forms a connection to both applied research and conservation. Thus the material from these proceedings contributes either directly or indirectly to all aspects of owls. Put another way, even though a particular contribution may deal only with basic research it can potentially impact work of land managers, wildlife specialists, conservationists, and others if they will make use of it.

One cannot only find much information in the content of the individual contributions but in the literature cited at the ends of the articles as well.

I would remind you that owls are a unique group of birds that are without equals in the specializations that they have evolved, enabling them to survive in a world of darkness. Our plenary speaker elaborated on that most thoroughly. I



Figure 1.--The pyramid of sound wildlife management. Basic research must form the foundation for management of either species or communities.

must qualify that, with regard to their surviving in darkness, having worked mostly on Asio flammeus a species that can be seen active either day or night, by pointing out that while there are some owl species that are very diurnal these are the exceptions rather than the rule. Owls represent only about 1.5% of all bird species thus reinforcing the idea that owls are unique and special. Because they have invaded a realm that is foreign to the diurnal humans they have been neglected with respect to being subject for study. Although they currently enjoy popularity amongst humans with their images being collected as statues, photographs, paintings, etc., they have been both dammed and deified in the millennia that they and man have coexisted. Because they operate in a world where man is in the dark, special techniques, apparatus, etc., are required to study them. We have seen techniques using light from the infrared portion of the EM spectrum. Perhaps light in the red segment of the visible light spectrum could also be used at least for some species. Also perhaps instruments that intensify available light, the so-called Starscopes, could be used, e.g., to minimize the risk of conducting direct observations from close range on the less timid species. Certainly radio telemetry, as we have seen at this conference, has played a key role in revealing some of the secrets that we have heard about here. No doubt it will play an even greater role in the future as the telemetry technology develops further, e.g., smaller species may be studied as smaller, lighter radios are developed. Lighter radios will also allow

tracing the migration routes, times, etc. of those species whose movements appear to be somewhat erratic in nature as well as the regular migrant species and perhaps satellite tracking would be most appropriate for some of these studies.

We have seen a number of different methods used in trapping owls [see the workshop presentations for details of numerous methodologies appropriate for owl research], some of them variations of techniques used on the diurnal raptors, i.e., hawks, falcons, etc., and some unique to owls. Successful trapping of owls is critical to many types of studies and I could not overemphasize the necessity of having known individuals while studying the basic ethology of the species in the field. At this point I will site a quote from Larry McKeever's new book "A dowry of owls"

Better one bird in hand than ten in the wood.
Better for birders, but for birds not so good"

I am sure those of you who have tried to trap owls can relate to this and would suggest that for the latter portion that depends on the professionalism of the biologist and the use that information gleaned as a result of the trapping is put to.

Management techniques have necessarily brought in habitat management. We are, I think, observing a shift in emphasis in management from the species to the community or even to the ecosystem. However, that shift in emphasis has yet to reach owl biologists [if the biologists are not looking at wildlife from that point of view how can conservationists and wildlife managers, as well as land managers, be expected to adopt that point of view?] for of 52 papers, 39 dealt with research on a single species, four dealt with two species and while there were seven papers dealing with more than two species only three of those dealt with community studies of owls. There may be occasions when the species approach is the only way

to go, e.g., in the case of endangered species [even in those cases the species does not exist in a biological vacuum but is interrelated with other species], but a more balanced approach is that of managing an ecosystem or segment of it. As we get a better picture of the detailed habitat needs of species we are learning that absolute minimum area dimensions for species are not the only thing required for management. We must know the quality of the habitat and, in many cases the configuration of the habitat is also crucial. This poses some interesting challenges for applied research, e. g., will a habitat segment with corridors leading from it to other tracts suffice with equal satisfaction to that of a larger intact area? Such points of view and questions are going to require manager-researcher teams for they require the expertise of specialists. The list of participants of this symposium identifies a good number of the owl experts [both professional biologists and serious amateurs doing professional calibre work] and hopefully these Proceedings will carry the challenge to those in a management position that deal with owls within the domain of areas that they manage!

We do not have reason to be complacent about our knowledge for any species of owl. This conference will however, I think, be viewed as a landmark in the history of owl biology for it [along with the symposium on owls held in Sacramento in the fall of 1985, and the paper session on rare owls at the World Conference on Birds of Prey to be held in Eilat, Israel on 22-27 March 1987] will go a long way toward identifying owls as a unique group of wildlife and owl researchers as being unique in their own "light." There has been considerable discussion about following up this symposium with another in two or three years with suggestions that it deal potentially with any of the owl species and that it be held in a locale that would attract biologists from parts of the world that have been much under-represented at this symposia, e. g., eastern Europe and Asia.

Evolution, Structure, and Ecology of Northern Forest Owls¹

R. Åke Norberg²

Abstract — In this introductory survey of northern forest owls I explore what distinguishes them structurally, ecologically, and energetically; what particular ecological conditions they are subjected to; and what selection pressures govern their evolution. Comparisons are made between communities of northern forest owls in the Old World and the New World; and between northern forest owl communities and more southern ones.

Forest owls, like most forest birds - and forest bats as well - have relatively short and broad wings, which are adapted for flight among vegetation. Their wing loading is low, which facilitates transportation of prey and also reduces the wings' aerodynamic noise.

Reversed sexual size dimorphism is very pronounced in some species of northern forest owls. But theories of this phenomenon must also explain the same dimorphism in tropical owls and in diurnal birds of prey, and must also be compatible with some notable exceptions from the general rule. These problems have often been ignored.

Forest owls are primarily "searchers" in the sense that they spend most of their hunting time searching for prey and little time pursuing and capturing them. They are "perch-and-pounce" hunters, but perch height, giving-up time, and flight length vary with sensory capacities, prey density, vegetation structure, and weather - aspects treated by optimal foraging theory.

Particular attention is given to the evolution of asymmetry of the external ears in some owls. Habitat choice, vegetation structure, and hunting technique dictate to what extent vision and hearing can be used for detection and localization of prey. Hearing is particularly useful in dense forest and for detection and localization of prey moving in dense ground vegetation or under snow. When an owl depends heavily on hearing for prey finding, demands on accurate vertical localization cause selection for vertical asymmetry of the external ears. But ear asymmetry results in conflicting auditory information at the two ears. This may require a "training period", with extensive head tiltings, in young owls before they can fully benefit from the ear asymmetry.

Interactions between owl populations and populations of small mammals are considered both in the ecological and evolutionary time scale. Owls specialized on small rodents tend to destabilize rodent population cycles, while generalized owls have a stabilizing effect, suppressing prey fluctuations. Both types of owls tend to synchronize population fluctuations of small rodents and other prey animals, both locally and over larger geographic areas. Rodent cycles give rise to different behavioral strategies in owls depending on their habitat choice, dietary specialization, hunting mode, sensory capabilities, and nesting habit.

1. INTRODUCTION

This symposium on the biology of northern forest owls was restricted from the outset to include only forest owls occurring partly or entirely north of latitude 35° North. As a brief remembrancer of

geography, 35°N is 11.5° N of the Tropic of Cancer which is at 23.5° N. The 35° N latitude crosses USA through southern California, central Arkansas, and the southern part of North Carolina. In the Old World it passes through the northernmost corner of Africa, through the Mediterranean Sea, just south of the Caspian Sea, through northern Tibet, and across central Japan. Any species occurring wholly below this 35° N latitude has not been considered a "northern forest owl".

By this criterion 22 owl species will be included (table 1). But apart from a brief mention below in a survey of owl distribution, some of these species are not treated further in any of the symposium contributions.

¹Paper presented at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

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I will open this introductory paper by a survey of the distribution of these 22 northern forest owls in North America, Europe, and Asia (table 1). Comparisons are made between communities of northern forest owls in the Old World and the New World.

Next I explore what distinguishes them structurally, ecologically, and energetically; what particular ecological conditions they are subjected to, and what selection pressures govern their evolution. I particularly consider various adaptations in owls for prey capture.

"Reversed sexual size dimorphism" is very pronounced in some species of northern forest owls, and I discuss this phenomenon in relation to the same dimorphism in tropical owls and in relation also to some notable exceptions among owls, which exhibit "normal sexual size dimorphism".

Forest owls are primarily "perch-and-pounce" hunters, and I consider their hunting modes in relation to optimal foraging theory.

Since asymmetry of the external ears is very common among northern forest owls, I pay particular attention to the function of ear asymmetry and to the evolution of ear asymmetry among owls in general. I particularly consider the ecological conditions promoting the evolutionary origin of ear asymmetry.

Interactions between owl populations and populations of small mammals are considered both in the ecological and evolutionary time scale.

Table 1. — The 22 species considered as northern forest owls in this "Northern Forest Owl Symposium". All species occur partly or entirely north of latitude 35° N. Species with asymmetrical external ears are denoted by *.

NORTH AMERICA	EUROPE	ASIA
<i>Otus flammeolus</i> Flammulated Owl	—	—
<i>Otus asio</i> Eastern Screech-Owl	—	—
<i>Otus kennicottii</i> Western Screech-Owl	—	—
—	<i>Otus scops</i> European Scops-owl	<i>Otus scops</i> European Scops-owl
—	—	<i>Otus brucei</i> Striated Scops-Owl
—	—	<i>Otus sunia</i> Oriental Scops-Owl
—	—	<i>Otus bakkamoena</i> Collared Scops-Owl
—	<i>Bubo bubo</i> * European Eagle-Owl	<i>Bubo bubo</i> * European Eagle-Owl
<i>Bubo virginianus</i> Great Horned Owl	—	—
—	—	<i>Ketupa blakistoni</i> Blakiston's Fish Owl
<i>Surnia ulula</i> Northern Hawk-Owl	<i>Surnia ulula</i> Northern Hawk-Owl	<i>Surnia ulula</i> Northern Hawk-Owl
<i>Glaucidium gnoma</i> Northern Pygmy-Owl	—	—
—	<i>Glaucidium passerinum</i> Eurasian Pygmy-Owl	<i>Glaucidium passerinum</i> Eurasian Pygmy-Owl
—	—	<i>Ninox scutulata</i> Oriental Hawk Owl
<i>Strix varia</i> * Barred Owl	—	—
<i>Strix occidentalis</i> * Spotted Owl	—	—
<i>Strix nebulosa</i> * Great Gray Owl	<i>Strix nebulosa</i> * Great Gray Owl	<i>Strix nebulosa</i> * Great Gray Owl
—	<i>Strix aluco</i> * Tawny Owl	<i>Strix aluco</i> * Tawny Owl
—	<i>Strix uralensis</i> * Ural Owl	<i>Strix uralensis</i> * Ural Owl
<i>Asio otus</i> * Long-eared Owl	<i>Asio otus</i> * Long-eared Owl	<i>Asio otus</i> * Long-eared Owl
<i>Aegolius funereus</i> * Boreal or Tengmalm's Owl	<i>Aegolius funereus</i> * Boreal or Tengmalm's Owl	<i>Aegolius funereus</i> * Boreal or Tengmalm's Owl
<i>Aegolius acadicus</i> * Northern Saw-Whet Owl	—	—
<div style="display: flex; justify-content: space-around; align-items: center;"> <div style="text-align: center;"> 12 (6°) ← 4 (3°) in common → </div> <div style="text-align: center;"> 9 (6°) ← 9 (6°) in common → </div> <div style="text-align: center;"> 14 (6°) ← 4 (3°) in common → </div> </div>		

Particular attention is given to rodent cycles and to the stabilizing and destabilizing influence of predation by generalized and specialized predators, respectively. Moreover, I consider the tendency that owl predation may have to synchronize population fluctuations among small rodents and other prey animals.

Throughout this introductory paper I will give some historical background to the various topics considered, and in particular to the historical development of new ideas and concepts.

2. DISTRIBUTION OF NORTHERN FOREST OWLS

2.1. A survey

The distribution of the 22 northern forest owls in North America, Europe, and Asia is summarized in table 1. It is based on Peters (1940) and Burton (1973). The "Working Bibliography of Owls of the World" by Clark, Smith, and Kelso (1978) also contains information on systematics and distribution. And this book is indispensable for all work on owl biology.

I will now survey the different species and make a brief comparison between communities of northern forest owls in the Old World and the New World.

There are three *Otus* species in North America, only one in Europe, and four in Asia. The flammulated scops owl *O. flammeolus* ranges through western North America down to Central America. It is closely related to the European and oriental scops owls, *O. scops* and *O. sunia* (all three of which are sometimes regarded as conspecifics; Hekstra 1973, p. 108). In North America, the eastern screech owl, *O. asio*, lives to the east of the Rocky Mountains, and the western screech owl, *O. kennicottii*, to the west of the Rockies. They are very closely related, interbreed locally (for instance in the Big Bend region of Texas, Marshall 1967, p. 3; Hekstra 1973, p. 101), and are sometimes considered to be conspecific. They are then referred to as *Otus asio*, the common screech owl, with the western population as a subspecies, *O. asio kennicottii* (Peterson 1961).

Among the four Old World *Otus* species considered here, *O. scops*, *O. brucei*, and *O. sunia* are all closely related, and are sometimes considered to be conspecific - and closely related to them is also the North American *O. flammeolus*, as mentioned above (Hekstra 1973, pp. 106, 108). The Old World collared scops-owl, *O. bakkamoena*, occurs in southeastern Asia up to about latitude 54° N. In a recent study of the territorial calls and of the wing of *Otus* owls in Pakistan, including *O. scops*, *O. brucei*, *O. sunia*, and *O. bakkamoena*, it was concluded that all four are indeed good species (Roberts and King 1986). The *Otus* owls thus constitute several species

groups whose systematics is difficult, and there has been considerable confusion concerning the taxonomic relationships of these owls. Geographic variation is extreme among screech-owls, and their coloration is complicated and has resulted from parallel and convergent evolution. Systematic treatments are given by Marshall (1967; 1978) and by Hekstra (1973).

Insects form the main diet of the *Otus* owls, and as a result most populations occurring north of the palm-limit are migratory. Exceptional in this respect is the common screech owl, *O. asio*, which is essentially resident throughout winter even in Canada, and then switches to non-insect prey like small mammals and birds. By contrast, the common scops owl, *O. scops*, in Siberia migrates about 7000 km south-east to Ethiopia (Hekstra 1973, p. 106), and mid-palearctic populations from 45-90° E, for instance from Mongolia, winter in Africa, south of Sahara (Moreau 1972, pp. 13, 194).

The Eurasian Eagle Owl *Bubo bubo* is a huge owl, the largest of all owls in the world. The weight of European owls is 2.2 - 4.0 kg for females (average 3.056) and 1.6 - 3.0 kg for males (average 2.275; Mikkola 1983). From these average weights of the two sexes, the overall average becomes 2.666 kg. This is twice as much as the mass of its American counterpart *Bubo virginianus*, which weighs only 1.309 kg (Mueller 1986, p.392).

Bubo virginianus relies heavily on the snow-shoe hare (=varying hare), *Lepus americanus*, for food. With its weight of 1.5 kg the snow-shoe hare is only about half as big as the European hares *Lepus timidus*, ca. 3 kg, and *Lepus europaeus*, ca. 4 kg. Likewise, the Canadian lynx, *Lynx canadensis*, and the smaller bobcat, *Lynx rufus*, which are other North American hare predators, weigh only about half as much as the European lynx, *Lynx lynx*. This suggests that the difference in size of the hares between North America and Europe has had some effect on the difference in size between the North American and the European *Bubo* owls and the lynx. But with *Bubo virginianus* the underlying causes must be more complex since it has a wide distribution throughout most of North and South America; therefore, insofar as size of the main prey selects for predator size, other prey than the snow-shoe hare must have affected the size of *Bubo virginianus* over a large proportion of its range.

Blakiston's Fish Owl, *Ketupa blakistoni*, is resident throughout the year in the boreal forest in eastern Asia. Its range extends up to latitude 60° N. There it occurs at streams and rivers that are so fast-flowing that they remain partially unfrozen throughout the winter. *Ketupa blakistoni* is the only fish owl with fully feathered legs, a feature undoubtedly associated with its northern distribution (Fogden, 1973, p. 68).

Leaving northern forest owl aside for a moment,

I will comment briefly on the world distribution of fishing owls. There are four species of *Ketupa* in Asia. They all have ear tufts and resemble *Bubo* owls. And in Africa there are three species of fish-owls of the genus *Scotopelia*. They lack ear tufts, and except for their specializations in common with *Ketupa* for eating fish, they are quite different in general appearance from the *Ketupa* owls. Nonetheless, owls from the two genera are believed to have their fish-catching specializations from a common ancestor rather than as a result of convergent evolution (Fogden 1973).

It is strange that there are no fish owls in the New World. There are a few species of fish-eating bats in tropical America, and it has been suggested that the presence of fish-eating bats has prevented fish owls from invading the New World or evolving there (Fogden 1973, p. 61). Let us examine this possibility in some detail.

So far, there are only five fish-eating bats known in the world (U. M. Norberg and Rayner 1987, who give further references). Australia has one, *Myotis adversus*, with mass 10.3 g. The European *Myotis daubentoni*, with mass 7.0 g, is mainly insectivorous, but has been reported to feed also on fish. The remaining three fish-eating bats have obvious adaptations in the wing and hind foot for fish-catching (U. M. Norberg and Rayner 1987). Among these, *Pizonyx vivesi*, mass 25 g, has a limited range on the southwestern part of the North American continent - in Baja California and Sonora, Mexico (Walker 1964). *Noctilio leporinus*, mass 59 g, ranges from Mexico southward to northern Argentina and Brazil, and *Noctilio labialis* (= *N. albiventris*) mass 30 g, occurs from Central America southward to Argentina. All five belong to the suborder Microchiroptera but are of mixed phylogenetic origins within it, with the genera *Myotis* and *Pizonyx* belonging to the family Vespertilionidae, and *Noctilio* to family Noctilionidae. Convergent evolution in behaviour and structure to fish-eating has obviously occurred among the fish-eating bats.

Even though the two South American fish-eating bats are larger than all the others, they are still very small by fish-owl standards and so take small fish, probably not heavier than about 50% of the mass of the bat, i.e. 30 g at most. It therefore seems obvious that the fish-eating bats cannot have constituted any competitive hindrance to an evolutionary origin of fish owls in the New World. The absence of fish owls from the New World thus seems to be one of those evolutionary results due to chance only; fish owls just have not happened to evolve in the New World, for no particular reason. An analogy among bats is the absence of blood-eating bats everywhere except from tropical America, where there are three species, each in a monotypic genus,

Desmodus rotundus, *Diaemus youngi*, and *Diphylla ecaudata* (Walker 1964).

The northern hawk owl, *Surnia ulula*, is circumboreal. It occurs along a broad zone of the northern coniferous forest, just beneath the edge of the arctic tundra, and ranges around the whole of the northern hemisphere. It hunts predominantly by eye and therefore depends on forests where the trees are widely spaced. This may be one reason for its northern distribution and for its choice of regions at high elevations above the sea level; forests on such ground are open and the coniferous trees are usually widely spaced and have typically narrow crowns, permitting good view of the forest floor.

The American pygmy-owl, *Glaucidium gnoma*, is very similar to the Eurasian pygmy-owl, *G. passerinum*, and is sometimes even considered conspecific with it (Ginn 1973, p. 178). *G. gnoma* has an elongated distributional range in the north-south direction, and occurs in western America, from southernmost Alaska southward to Guatemala in Central America. *G. passerinum* also occurs along an elongated distributional band but with an east-west orientation and a width of 600 to 1000 km.

Strix varia and *S. occidentalis* are two exclusively New World *Strix* species, which are confined to North America except for *S. varia*, whose range extends southward into Central America. They have largely non-overlapping ranges, extended in the north-south direction, *S. varia* occurring to the east, and *S. occidentalis* to the west of the Rocky Mountains. *S. occidentalis* has a strong preference for unlogged forests of mature or old-growth conifers more than 200 years old, forming uneven-aged, multilayered canopies with closures of 65-80% (Forsman, Meslow, and Wight 1984, p. 16).

Strix nebulosa is circumboreal occupying much the same range as does the hawk owl, *Surnia ulula*. *S. nebulosa* is the largest of all *Strix* owls, and in North America as well as in Eurasia its distribution is north to those of the other *Strix* species. In North America its distribution overlaps only the northernmost parts of the ranges of *S. varia* and *S. occidentalis*.

In the Old World, *S. aluco* and *S. uralensis* are ecological equivalents to *S. varia* and *S. occidentalis* in North America. But in Eurasia the ranges of all three *Strix* owls are extended in the east-west direction and ordered from north to south with the largest one, *S. nebulosa*, furthest to the north, followed in latitudinal range by the medium-sized ural owl, *S. uralensis*, and then by the smaller tawny owl, *S. aluco*, furthest to the south. This is a fairly orderly pattern even though there is considerable overlap between the ranges of *S. nebulosa* and *S. uralensis*, and rather less overlap between *S. uralensis* and *S. aluco* (Svårdson 1949; Lundberg 1980).

The Eurasian *S. uralensis* and *S. aluco* are two closely related but very well defined species of markedly different sizes and with essentially non-overlapping ranges, as described above; *S. uralensis* (female mass 871 g, male mass 720g) occupies mainly the coniferous taiga and *S. aluco* (mass 583 g and 474 g; Mikkola 1983, p. 377) occurs further south in semi-open and open deciduous woodland. But after crossing a female *S. aluco* with a male *S. uralensis* in captivity, Scherzinger (1983) made the remarkable discovery that fertile eggs were produced and even gave rise to two viable young, a female and a male. The F₁ hybrid progeny exhibited a mosaic of characters from their parent species as regards size, coloration, and vocalization, the overall result therefore being truly intermediate. The male and female hybrid siblings did not produce any eggs during the two years they shared cage, but the hybrid male later gave rise to viable F₂ birds in back-crosses with both parent species, with *S. aluco* as well as with *S. uralensis*.

The long-eared owl, *Asio otus*, is circumboreal with a range extending across North America and Eurasia in a broad belt essentially south of the range of the hawk owl, *Surnia ulula*.

The boreal owl (North American name), or Tengmalm's owl (European name), *Aegolius funereus*, is circumboreal and occurs in a wide belt of the northern coniferous forest, beginning as far north as the hawk-owl's range, but extending much farther south. The range of the smaller saw-whet owl, *Aegolius acadicus*, is strictly limited to North America (unless the Central American *Aegolius ridgwayi* will prove eventually to be merely a subspecies of *A. acadicus*). *A. acadicus* occurs essentially south of the range of *A. funereus*, but there is a zone of overlap along the Canadian-USA border. Despite the more southern range of *A. acadicus*, northern populations of it are more migratory than is *A. funereus*. The latter performs irregular, irruptive, movements only, in North America as well as in the Palearctic.

2.2. Conclusion and discussion

As will have been apparent, the northern forest owl faunas in North America, Europe, and Asia are remarkably similar in their overall composition (table 1).

Four species are circumboreal and occur in all three regions, viz. *Surnia ulula*, *Strix nebulosa*, *Asio otus*, and *Aegolius funereus*.

There are three *Otus* owls in North America, one in Europe, and four in Asia, and none of these occurs both in North America and Eurasia.

Bubo and *Glaucidium* both have a different representative in North America and in Eurasia, and there is a remarkable size difference between the two *Bubo* species.

The fish-owl *Ketupa blakistoni* occurs only in Asia, and the total absence of fish-owls from the New World has no obvious ecological explanation, but is probably the result of chance only; simply that no fish owls did ever evolve in the New World. One possibility in terms of ecological explanation could be if *Bubo virginianus*, which is a generalized owl with a very wide diet, does take fish to the extent that it fills the prospective niche of any fish owl.

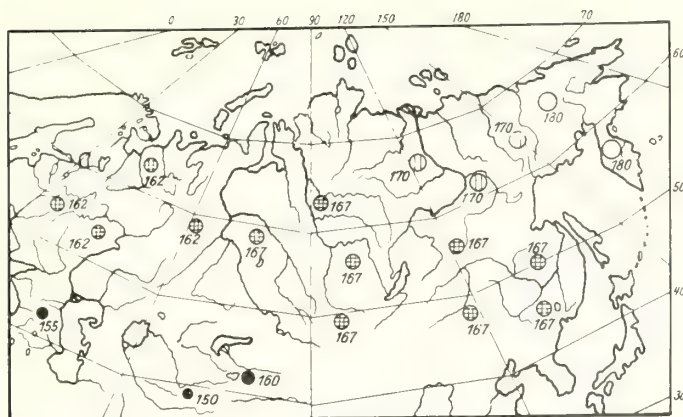
Strix nebulosa is shared between all three regions, while there is a different set of two additional, *Strix* species in North America and Eurasia, *S. varia* and *S. occidentalis* versus *S. aluco* and *S. uralensis*, all four of which are structurally and ecologically similar.

Finally, *Aegolius funereus* occurs in all three regions, whereas *A. acadicus* is unique to North America. The reason why North America has two *Aegolius* species, and Eurasia only one, may be that *Aegolius* probably evolved in the New World. My reason for believing this is that there are four *Aegolius* species in the New World as opposed to only one in Eurasia; *A. funereus* and *A. acadicus* in North America, *A. ridgwayi* in Central America, and *A. harrisii* in South America, but only *A. funereus* in Eurasia.

The distributional patterns of *Strix* owls in Eurasia and *Aegolius* owls in North America thus are in accordance with Bergmann's ecogeographic rule, the tendency for body size in homeotherms to be negatively correlated with environmental temperatures, i. e. for body size to be larger where temperature is lower. This trend may be expected for the distribution of populations of differently sized animals of the same species (fig. 1), or for the distribution of differently sized species that are closely related and ecologically similar (as with the *Strix* and *Aegolius* species).

Among the 124 (or so) species of owls in the world, 42 species - or 34% - have asymmetrical external ears. Among the 22 northern forest owls recognized here, nine - or 41% - have asymmetrical external ears. They are marked with an asterisk in table 1. Among the 22 northern forest owls the proportion of species with asymmetrical ears in the three geographic regions is 50% for North America, 67% for Europe, and 43% for Asia. The percentage (41%) for all northern forest owls taken together is lower than the percentage for the owls of any of the three geographic regions taken separately. The reason is that owls with asymmetrical ears tend to occur in two or three of the geographic regions more often than do species with symmetrical ears. These large geographical ranges of species with ear asymmetry may reflect greater ecological success than for those with symmetrical ears.

The figures 50%, 67%, and 43% for the northern, regional, proportions of the number of owls with ear asymmetry are to be compared with 34% worldwide.



○, ⊙, ⊕, ●, ● = Increasing darkness of plumage.

Figure 1. - Geographic variation in size and coloration in *Aegolius funereus* in the Palearctic in accord with Bergmann's and Gloger's ecogeographic rules. There is a trend of increasing size towards the north and northern owls have less plumage pigmentation than more southern ones. The length of the hand-wing is given in millimeters at the circles whose size is also proportional to wing length. The different shades of the circles symbolize plumage darkness of owls from various local populations. - From Lüers and Ulrich (1959, p. 644).

So ear asymmetry is a common characteristic among northern forest owls. Therefore I will devote some space below to explaining the function of ear asymmetry in owls, to exposing the multiple evolutionary origins of ear asymmetry, and to considering the selective forces leading to its origin.

3. COLOUR MORPHISM

Most screech-owls are dimorphic in colour (Marshall 1967, p. 1). The North American screech owl *Otus asio* (and in particular the Nevada Great Basin population *O. a. macfarlanei*; Peterson 1961) occurs in two distinct colour phases, grey and brown, but also in one or more intermediate forms.

The ecological significance of the various colour phases were recognized as early as 1893 by Hasbrouck. Based on a sample of about 3600 owls, he concluded that the frequencies of the various colour morphs are independent of age, sex, or season, but that temperature and humidity affect the frequency distribution of the various colour morphs. Martin (1950) recognized nine colour morphs in a sample of 145 owls from Canada, and, like Hasbrouck (1893), found no relationship between colour and sex.

Laurel VanCamp and Charles Henny (unpublished, cited from Mosher and Henny 1976) found overwinter survival to be higher for grey than for red *Otus asio* owls in one unusually severe winter in northern Ohio (44% more red birds dying), whereas there were no differences in normal winters. Mosher and Henny (1976) recorded oxygen

consumption at different ambient temperatures and showed that red-phase *Otus asio* had significantly higher metabolic rates at temperatures below -5°C , whereas there was a tendency for the red-phase owls to consume less energy above about 5°C . The differences may be associated with colour either directly, due to differences in plumage conductance or heat radiation, or indirectly, via fundamental physiological differences genetically linked with plumage colour.

The colours of the various morphs or phases are genetically fixed for the lifetime of the individual. The genetic basis of the colour morphs has been studied in *Otus asio*. Hrubant (1955) concluded that if three colour morphs are distinguished, the outcome of 80 matings in a population of free-living Eastern screech owls in Ohio is consistent with the inheritance via three alleles at one autosomal gene locus, and with a graded order of dominance of red over intermediate over grey.

The Old World *Strix aluco* does also occur in different colour phases, which occur together in local populations. There is a continuous gradation from extreme grey, through tawny, to red phenotypes (Kjell Wallin, Göteborg University, pers. comm.; own observations), which suggests a polygenic basis of plumage colour.

4. GEOGRAPHIC VARIATION IN COLOUR

Writing about the coloration of *Otus* owls, Marshall (1967, p. 2) emphasized its cryptic nature and the frequent evolutionary convergence in cryptic coloration. Species after species accomplish the same trends even on different continents. Where two or more species are sympatric, their coloration is almost identical. He interpreted this to be the result of strong selection from predators.

In *Otus* there are consistent geographic and climate-related trends in coloration from rich dark brown in humid areas of the north to grey in deserts and to rufous in the tropics, and they all have their blackest form at or near arid country of high altitude. The rufous phase was believed to match the colour of red-barked trees, which actually occur in the tropics (Marshall 1967, p. 2). All these colour variations were considered by Marshall to be the result of strong selection for concealment by the action of both diurnal and nocturnal predators on owls.

With reference to the differences between grey and red morphs of a single species in their metabolic energy costs at different ambient temperatures (described in the previous section; Mosher and Henny 1976), I suggest that the geographic and climate-related, intra-specific, variation in colour of locally monomorphic species is the result of local selection for minimization of metabolic energy costs for thermoregulation.

There are thus two hypotheses to explain the geographic and climate-related, intra-specific, colour trends in owls; (1) it is the result of natural selection for cryptic coloration against the prevailing local colour of bark, twigs, and leaves (Marshall 1967, p. 2), or (2) the result of natural selection for a colour that reduces the metabolic energy costs of thermoregulation under the local climate conditions. Actually, these two hypotheses need not be mutually exclusive.

Marshall (1967, pp. 2, 3) suggested that *Otus* owls are monomorphic where the colour of the vegetation is monotonous but that they occur in various colour morphs where the vegetation is varied, favouring different cryptic coloration in different localities and at different times of the year. Likewise, it might be argued that if the colour is selected to minimize thermoregulatory metabolic energy costs, monomorphism may occur where climatic conditions are stable whereas polymorphism is favoured where there are large local and temporal variations in climate.

These geographic colour variations are examples of a fairly general phenomenon among animals, summarized in Gloger's ecogeographical rule. This rule is based on empirical observations within species but on populations in different geographic regions. Gloger's rule states that animals in warm and humid areas are more heavily pigmented than those in cool and dry areas, and black pigments are reduced in warm dry areas, whereas brown pigments are reduced in cold humid areas (Mayr 1965, p. 324). I know of no other explanation of the rule except for (1) the crypsis and (2) the thermoregulatory hypotheses discussed above.

In Eurasia *Aegolius funereus* shows a consistent clinal trend in size and coloration in accord with Bergmann's and Gloger's rules, respectively (fig. 1; Lüers and Ulrich 1959, p. 644). Gloger's rule seems to be broadly applicable also to inter-specific comparisons of plumage colours among non-migratory northern forest owls; the northern *Strix nebulosa*, *Strix uralensis* and *Surnia ulula* are light and grey and with very little brown colour while more southern owls, like *Strix aluco* and *Asio otus* are darker and with much brown in their plumage.

5. GENERAL SHAPE AND FORM OF FOREST OWLS

5.1. Body form

Wood owls in general, and those occurring at high latitudes in particular, are very stocky, or chunky, and have a very loose, fluffy, and thick plumage (fig. 2). In this respect they differ from owls hunting largely on the wing in open country.



Figure 2. - Plumage thickness is probably the result of an energetic compromise between thermoregulation and flight. Minimization of energy cost for thermoregulation when the ambient temperature is below the bird's thermoneutral zone selects for thick plumage, while minimization of flight cost selects for thin plumage. Forest owls fly relatively little and have a thick, fluffy, plumage. This old picture shows a tawny owl, *Strix aluco*. - From Brehm (1922, Vol. 8, p. 224).

I will briefly consider the costs and benefits to owls of having a thick plumage. The main benefit must be (1) improved thermal insulation, which reduces the metabolic energy costs for thermoregulation when the ambient temperature is below the owl's thermoneutral zone. And there are two main costs, (2) the cost of growing the additional downs and feathers and (3) the extra energy cost of flight because of increased aerodynamic body drag and because of the added plumage weight, albeit small.

Points (1), (2), and (3) probably identify the most important selection forces governing plumage thickness in owls. The cost of growing a thick plumage (2) cannot profitably be compared with the other costs because they are incurred at different time periods in the bird's life. The plumage thickness actually observed in a species instead is probably the result of a compromise mainly between the conflicting demands for minimization of metabolic energy costs for thermoregulation (1) and for flight (3). The balance between these costs should be most critical in winter.

Now, for a bird that flies much, the optimum

plumage thickness is less than for a bird that flies less. But in a cold environment, the optimum plumage thickness is greater than in a warmer environment.

These predictions seem to be borne out by a comparison of different owls; those that live far to the north (cold environment) and fly little has a thick plumage, *Strix nebulosa* being an extreme example of this category, while owls that live further to the south, or that are migratory (warm environment), and fly much, for hunting and/or for migration, have a slim appearance, as for example *Asio otus* and *Asio flammeus*.

The penalty from thick feathering comes in the form of increased metabolic energy costs of flight. But forest owls do not fly very much. Therefore, the balancing selection pressures for improved thermal insulation (i.e. thick plumage) and reduced flight costs (i.e. slim plumage) balance at a rather thick plumage.

It should be noted that thick plumage is an adaptation for winter conditions. In summer it may cause difficulties for the owls getting rid of excessive heat (e.g. Barrows 1981); then gular flutter and other means of dissipating body heat consume extra energy, rather than conserving it.

5.2. Head size and shape

The owls have big heads for two good reasons; to accommodate the huge eyes, adapted for vision in poor light, and to enable the external ears to be big and to be placed far apart, both factors contributing to proficiency in sound localization (see section on hearing). And since the head is large anyway in owls (i.e. for these particular reasons), the body located aft of it in flight may as well be stocky since it does not add much to the aerodynamic drag, provided it does not extend outside the frontal projection of the head. Aerodynamic drag is determined primarily by the projected frontal, cross-sectional, body area.

Open-country owls which fly much, like *Asio otus* and *Asio flammeus*, have a slimmer appearance than forest owls; and it is not only the overall body form that is slimmer, but they also have relatively much smaller heads than the forest owls.

Diurnally hunting owls and open-country owls tend to have distinct eye-brows, whereas eye-brows are small or virtually lacking in nocturnal forest owls. For example, contrast *Surnia ulula* and *Glaucidium* with *Strix* and *Aegolius* species! The eye-brows obviously function as a protection against the glaring light from the sun, sun-lit clouds, and the open sky.

5.3. Ear tufts

Ear tufts occur in the *Otus* and *Bubo* species, in *Ketupa blakistoni* and in *Asio otus*. They function as

camouflage at the day roost; the owls usually erect the ear tufts when trying to avoid being detected and at the same time make themselves appear narrower by compressing the plumage, stretching upwards into an erect posture, and sometimes also turning its nearest shoulder towards the intruder, thus presenting a disrupted colour pattern, with the wings forming a dark region contrasting with the generally lighter breast. This is an effective way of camouflage, and the erected ear tufts likewise have a disruptive effect on the general appearance of the owl, making it blend better with the surroundings. Ear tufts are particularly common among forest owls, lending support to the camouflage hypothesis, because it is among branches and twigs that ear tufts are most effective (Perrone 1981).

But ear tufts have also been supposed to be a kind of mimicry; when erected, the ear tufts may make the owl face resemble that of a mammalian carnivore, which supposedly intimidates a prospective attacker (Myserud and Dunker 1979). The camouflage and the carnivore-mimicry hypotheses are not mutually exclusive but might well operate together.

6. WING SIZE AND SHAPE

The wing loading, which is total weight Mg divided by wing area S , is very low in owls as compared with other birds (M is mass and g is acceleration due to gravity). Since wing area scales with body mass as $M^{2/3}$ in geometrically similar birds, the wing loading Mg/S scales as $M^{1/3}$. Therefore, for geometrically similar birds, wing loading becomes larger with increasing size of bird. But the effect of size can be compensated for by calculating a "relative wing loading", which is wing loading divided by $M^{1/3}$, or $Mg/(SM^{1/3})$. And when this is done, owls are also among the birds with the lowest relative wing loading (Norberg and Norberg in press).

Any characteristic flight speed, such as the minimum power speed or the maximum range speed (identified by their characteristic locations along the U-shaped power versus speed curve) varies with the square root of the wing loading, or as $(Mg/S)^{1/2}$ (Lighthill 1977; U. M. Norberg 1985, p. 138). Because of their low wing loading, owls can fly slowly. This has two advantageous consequences: (1) owls can make sharp turns, which is useful in dense vegetation, and, because of the low relative speed of the air flow over the wings, (2) there is less tendency for aerodynamic noise to be produced, facilitating hearing while in flight and making it more difficult for prey animals to detect an approaching owl.

There are additional advantages of low wing loading to predators like owls; owing to the initially low wing loading, the loading during prey transport tends to be low also for the owl and prey combined.

This should enable the owl to fly slower during transport of prey of a given weight, therefore (3) reducing the power output during prey transport in flight and also retaining the owl's manoeuvrability, of particular importance in forest. For the same reason, given a maximum, sustainable power output, (4) the owl should be able to transport heavier prey (Norberg and Norberg in press), because with higher wing loading the flight speed would need to be higher with ensuing larger demands on power output.

Aspect ratio is an aerodynamically important measure expressing the ratio between wingspan and the average wing chord. It can be conveniently estimated in animals as wingspan b squared divided by wing area S , or b^2/S , which is wingspan divided by mean chord length c since $S = bc$. As compared with other birds, owls have wings of low aspect ratio, i. e. short and broad wings (Norberg and Norberg, in press). And among owls themselves, forest species generally have much lower aspect ratios than open-country owls. The short, broad wings of forest owls are advantageous for flight within dense vegetation for the obvious reason that the flying owl needs less space among branches and twigs, but also because such wings enhance manoeuvrability (Norberg and Norberg in press). With a short wingspan, the wing chord needs to be long for the wing loading to remain low, and this is a reason why forest owls have low aspect-ratio wings.

7. SILENT FLIGHT - DAMPING OF AERODYNAMIC NOISE

There are two reasons why owls benefit more from silent flight than would most other birds; (1) it increases the probability for an owl to approach and pounce upon a prey with acute hearing, like small mammals, without being detected acoustically; and (2) it improves the ability of the owl to detect and localize sound in flight, since flight noise would mask other sounds.

In an insightful paper in 1934, Graham saw an association between the silent flight of owls and the following three structural features of flight feathers.

(1) The leading edge comb. - There is a remarkably stiff, comb-like fringe on the front margin of every feather that functions as a leading edge. When there is a graded length of the anteriormost primary feathers, the ones behind the first feather are combed in the distal region that extends beyond the first feather (fig. 5). Likewise, where a feather is emarginated, there is a combed fringe on the new, secondary leading edge behind the slot. This comb was believed to reduce noise by its effect on the pressure distribution in the boundary layer behind the leading edge.

(2) The trailing edge fringe. - Along the trailing edge of the wing there is a very soft hair-like fringe

on the primary and secondary feathers. The barbs in the fringe are exceedingly flexible and do not form a continuous vane but are free to separate.

Silencing probably comes from the fringe's smoothening effect on the air flow at the trailing edge where the airstreams along the lower and upper wing surface mix. The stream along the ventral surface of the wing has a higher pressure and velocity than the stream over the wing. The fringe may also suppress flutter, accompanied by sound, in this region of air mixing.

(3) The downy upper surface. - The upper surface of the primary and secondary flight feathers are covered with a fine and soft velvet-like lining of short hair-like structures. It reduces the noise made by feathers sliding over one another as the wings are extended and flexed throughout the wingbeat.

Apart from these three features of owls Graham (1934, p. 843) recognized one more, in passing, namely:

(4) The generally low wing loading of owls, which enables them to maintain small angles of attack and relatively low speeds of the distal wing parts throughout the wingbeat. As a consequence, there is less opportunity for aerodynamic noise to arise as the air passes relatively slowly past the sharp leading edge of the anteriormost flight feathers. Likewise, because of the lower pressure difference between the lower and upper wing sides, there is less abrupt pressure equalization at the trailing edge of the wing and at the wingtip, entailing less noise.

Fishing owls, both *Ketupa* and *Scotopelia* (Graham 1934; Thorpe and Griffin 1962), generate flight noise and also lack the structural characteristics associated with silent flight. Thorpe and Griffin (1962) showed that the flight of owls is silenced not only in the frequency range audible to man, but also in an ultrasonic range above 15.000 Hz, again with the notable exception of the fishing owls *Ketupa* and *Scotopelia*, which produce more flight noise also in this frequency range than do other owls of similar sizes. The ears of small mammals are sensitive to such ultrasonic frequencies, so flight silencing in this region is also essential to owls, even if these frequencies are more attenuated with distance and therefore do not carry as far as does sound of lower frequencies.

Further descriptions of the silencing structures of owl feathers appear in Sick (1937, pp. 316-321), Hertel (1966), and Neuhaus, Bretting and Schweizer (1973). Neuhaus et al. (1973) and Gruschka, Borchers and Coble (1971) examined the frequency spectrum and sound pressure levels of the flight noise produced.

8. REVERSED SEXUAL SIZE DIMORPHISM

8.1. introduction

Sexual size dimorphism of the "normal" kind,

with males larger than females, was explained by Darwin (1871) as a result of sexual selection favouring large males in competition over mates. "Reversed" sexual size dimorphism refers to female dominance in size. It occurs among two categories of birds. Species in one of these are characterized by having reversed roles of the sexes in pair formation, females competing for males. Therefore this size dimorphism can also be explained by sexual selection. Such species occur, for example, among Charadriidae and Scolopacidae.

The second category, which is of more concern in this paper, includes most raptors (Falconiformes), owls (Strigiformes) and skuas (Stercorariinae). In addition to the reversed sexual size dimorphism, the mates have markedly different roles during breeding in these predatory birds. The female usually incubates and later stays in or near the nest, guarding the offspring until they are more than half-grown, while the male forages for the whole family (Andersson and Norberg 1981).

The degree of dimorphism varies strongly among species, and there is a clear across-species trend with dimorphism being most pronounced in species with the largest proportion of agile prey in their diet (Earhart and Johnson 1970; Reynolds 1972; Snyder and Wiley 1976; Newton 1979, pp. 19-27). The European sparrowhawk, *Accipiter nisus*, shows a greater weight difference between the sexes than any raptor in the world, the female being 1.7-1.9 times as heavy as the male (fig. 3) (Opdam 1975; Newton 1986, p. 32). And among owls, the most pronounced size dimorphism occurs in *Aegolius funereus* and *Strix nebulosa*, in which the female is 1.38 - 1.57 times as heavy as the male (Earhart and Johnson 1970, pp. 254, 255, 259; Lundberg 1986, p. 135; Korpimäki 1986, p. 327).

The explanation of reversed sexual size dimorphism in predatory birds has been lively debated recently, and there is disagreement about the underlying causes. Reviews occur in, for instance, Newton (1979, pp. 19-27; 1986, pp. 32-34, 323-326), Andersson and Norberg (1981), Mueller and Meyer (1985), and Mueller (1986), the latter two containing extensive tests of predictions from the main hypotheses. Owls are treated in, for instance, Earhart and Johnson (1970), Snyder and Wiley (1976), and Mueller (1986).

The first and most important requirement on a theory explaining the evolutionary origin of reversed sexual size dimorphism is that it should apply to all three groups of predatory birds with reversed sexual size dimorphism, viz. to raptors, owls, and skuas; and it should be applicable in all parts of the world. It should also be able to cope with the few, but notable, exceptions to the rule, i. e. to species showing normal size dimorphism. Examples of such species among owls are the burrowing owl, *Speotyto (Athene) cunicularia*, and several owls of the genus *Ninox*.

I shall now review the basic features of an eclectic theory, with many new elements in it, presented by Andersson and Norberg (1981). They strongly emphasized the need for such a theory to provide explanations at three levels, denoted A, B, and C below and in figure 3.

A. Why is there such a marked role partitioning between the sexes among these birds during the breeding season?

B. What determines the direction of the role partitioning and size dimorphism, i. e. why does the male alone take on the role as food-provider for the whole family during most of the breeding season?

C. What determines the degree of size dimorphism which varies strongly among species? Andersson and Norberg also stressed that a theory must explain why the factors invoked apply more to predatory birds than to others.

The explanation presented by Andersson and Norberg (1981) is ecological, and their various arguments are numbered 1 - 15 below and in figure 3 (their paper should be consulted for references to those arguments that are from other sources). They emphasized conditions during breeding (Andersson and Norberg, 1981, their legend to figure 4); since the differences in size and behaviour are sexual, the underlying causes are probably linked to aspects of breeding and to prey choice during breeding (stressed later also by Newton, 1986, p. 33).

A. (1) Owing to their structural and behavioural adaptations for prey capture, entailing fighting 'know-how', birds of prey and skuas should be more successful than similarly sized, non-predatory birds in defending offspring. (2) When the prey are vertebrates, which have acute senses to detect predators, and when two predator mates hunt in the same territory (but without co-ordinating their search), one mate may often be searching where the other has recently alerted potential prey. Because of this interference they may not procure much more food together than would one mate alone, using systematic search.

These arguments may explain why separation of breeding duties may be particularly advantageous among predatory birds, leading to its evolution in the first place.

B. The following features may explain the direction of role partitioning and size dimorphism, i. e. why the female stays at the nest and becomes the larger sex, not the male. (3) There is a risk of damage to the developing eggs inside the female during hunts (Walter 1979); (4) the added weight during egg production reduces her flight performance in hunts; (5) the female has to visit the nest for egg laying; (9) "courtship feeding", widespread also among non-predatory birds, obviously speeds up energy accumulation by the female for egg production and also enables her to conserve energy by not hunting. -

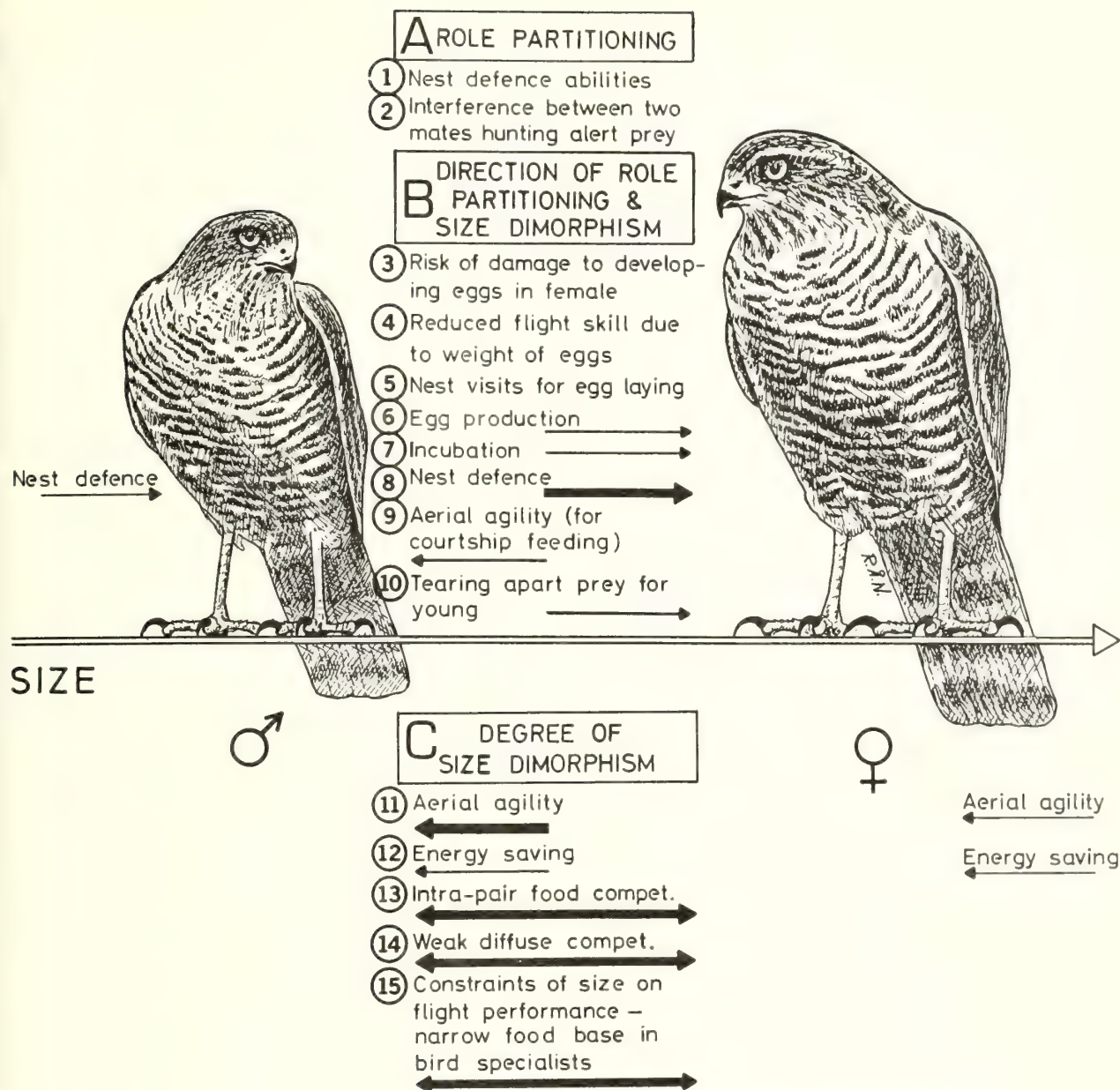


Figure 3. - Direction and relative importance (thickness of arrows) of hypothetical selection pressures that may be responsible for the sex role partitioning and reversed sexual size dimorphism among raptors, owls, and skuas. The figure shows a male and a female sparrowhawk, *Accipiter nisus*, drawn to the same scale. This Old-World hawk is the most size-dimorphic raptor in the world, the female being 1.7 - 1.9 times as heavy as the male. For this figure the weight ratio was taken to be 1.7, and assuming that geometric similarity prevails, this corresponds to the length ratio 1.2 shown. The explanation in this figure emphasizes three levels. - Modified from Andersson and Norberg (1981, p. 121).

which tends to predispose the female for the non-hunting role among birds of prey (fig. 3). These were reasons for the direction of role separation, while the following points, (6) - (10), may explain the direction of size dimorphism.

(6) Egg production, (7) incubation, (8) nest defence and (10) the dividing up of food for the young select for large female size, roles (8) and (10) probably most often falling on the female which attends the nest while the male is away hunting. And courtship feeding by the male (9) selects for small male size, but this needs some explanation.

Andersson and Norberg (1981) made a scaling analysis of six aspects of flight performance that must be crucial for hunting success. The only flight function which improves with increased predator

mass is terminal diving speed, but its dependence on mass is weak. In the other five respects a small bird does better than a larger, but geometrically similar, one. This applies to (i) maximum linear acceleration in flapping flight, (ii) maximum speed in horizontal flapping flight, (iii) maximum rate of climb in flight, (iv) maximum angular roll acceleration, and (v) turning ability, the latter two aspects governing manoeuvrability. Features i - v together should be of overriding importance, in relation to the terminal speed in dives, in determining the best predator size for hunting. By linear programming, Andersson and Norberg (1981) illustrated how this set of five flight aspects may constrain predator size, favouring small over large.

(9) Courtship feeding by the male selects for aerial agility, therefore tending towards small males.

C. The following aspects may be important for the various degrees of dimorphism in different species. The more agile the prey is, the closer the predator should approach the prey size limit below which subduing and transporting the prey become difficult. The more mammals and birds the predator takes, the stronger the selection for small size therefore becomes, given a particular size range of prey, constrained downwards and upwards by smaller and larger competing predators. (11) Since the male does most of the hunting, he is more strongly selected for small size than the female, and more so the more agile prey he takes. (12) A small male also expends less energy than a larger one, in particular among species with active hunting modes, which are associated with high energy costs for locomotion, as in predators on mammals and birds. The less energy that the male expends himself the more of the prey that he catches can be diverted to the young, which selects for small size and small fat reserves (R. Å. Norberg 1981).

(13) Intra-pair food competition should tend to drive the sizes of female and male apart. This applies in particular to bird specialists (15), which have narrow size spectra of potential prey, their food base therefore being prone to depletion. Their prey-size range is narrow because they can outfly and catch only prey birds that are large relative to themselves, whereas birds which they can outfly more easily tend to be too large for them to subdue and transport to the nest. Because of the narrow food base of each sex in predators specialized on birds as prey, such specialists thus should be subjected to particularly strong selection to alleviate intra-pair food competition by evolving a high degree of size dimorphism, which widens the combined prey base of the predator pair.

(14) Among predators on birds there should be weak 'diffuse' competition (from competitors of similar as well as of different kinds) because very few but the most specialized birds of prey can catch birds. Therefore there should be relatively little

competitive resistance against evolutionary divergence of the food-size niches of female and male among such birds, facilitating evolutionary divergence in size.

Among the various flight characteristics considered above, (i) maximum linear acceleration in flapping flight and (ii) maximum speed in horizontal flapping flight, may be of some importance to *Glaucidium* owls, which may take birds in flight, but not so much to other owls. But the two aspects that govern manoeuvrability, i. e. (iv) maximum angular roll acceleration, and (v) turning ability, should both be important for the hunting success of most owls. And this should apply in particular to forest owls, and most so to those hunting in dense forest, where good manoeuvrability in flight among vegetation is indispensable.

Indeed, sexual differences in manoeuvrability due to differences in mass and wing size may lead to sexual differences in diet and habitat utilization, small males being more able to exploit dense forest (Korpimäki 1986). Dietary differences might arise directly, from different, size-related, hunting abilities, or indirectly, from different, size-related, habitat utilizations. Females of *Strix nebulosa* and *Aegolius funereus* take larger prey than do males (Mikkola 1983, p. 378).

Since selection for manoeuvrability should be stronger in the male than in the female, because the male does most of the hunting, the degree of sexual size dimorphism in the set of characters that governs manoeuvrability should be positively correlated with the vegetation density in the hunting habitat (R. Å. Norberg in prep.). This may help explain why *Aegolius funereus* and *Strix nebulosa*, both of which fly much in dense forest, are the most size-dimorphic of all owls.

There seems to be a widespread misconception about the proportion of birds in owls' diet and their need for manoeuvrability (e. g. Lundberg 1986, p. 136); with the exception of *Glaucidium* owls, which may take birds in flight, most other owls probably take their avian prey on the night roost. This does not favour manoeuvrability as much as do aerial chases.

There is one aspect of small size among owls that might reduce hunting efficiency, namely the reduced distance between the ear openings; it leads to reduced accuracy of sound localization using time cues. Obviously there is selection to obviate this disadvantage of small male size, because in *Bubo virginianus* at least, skull width is larger in the male than in the female, whereas females are larger in all other measurements (McGillivray 1985).

The normal size dimorphism in *Speotyto cunicularia*, with males larger than females, actually supports the Andersson- Norberg theory (1981, p.112). This owl uses open habitat

where the male can easily detect approaching predators whereas the female, from within the subterranean nest burrow, can not. It seems natural, therefore, that the male should guard and defend the nest by aerial attacks. Moreover, *Speotyto* is the only North American or Eurasian owl with colonial breeding, and it is known to engage in group defence against predators, which further reduces the need for females to be the larger sex (Mueller 1986, p. 399). This supports the nest-defence argument for role partitioning in point A:1 in figure 3. But the *Ninox* owls remain an enigma for all hypotheses on reversed sexual size dimorphism among predatory birds (Andersson and Norberg 1981, p. 120).

Lundberg (1986) focused on northern owls only, observed that the degree of dimorphism in mass is inversely correlated with environmental temperature, and argued that because cold climate and early breeding should select for large females (who do the incubation), leading to strong dimorphism, the degree of mass dimorphism is explained by the environmental temperatures. I agree this may help explain the degree of mass dimorphism. But Lundberg (1986) ignored tropical owls and raptors, as well as the exceptional species; and he did not explain why role partitioning occurs (A; fig. 3) and what determines the direction of role partitioning and size dimorphism (B), and so his hypothesis lacks the generality that any such theory must exhibit.

An additional argument by Lundberg was that because prey brought by male owls to nest-attending females are large (as compared with those of non-predatory birds), they tend to be delivered at long intervals; and under harsh and fluctuating weather conditions the intervals become unpredictable. Since large females take longer time to starve than small ones, Lundberg (1986, p. 138) thought that large female size is selected for under such conditions. But a large female needs more food than a small one, and since temporarily surplus prey are routinely stored in the nest among most owls, a small female should survive longer on given rations of food, delivered at unpredictable intervals (fig. 21).

Korpimäki (1986, p. 328, 329) observed that early breeding pairs of *Aegolius funereus* in Finland were more dimorphic in weight (but not in hand-wing length) than later breeders. Because of the "calendar effect" - clutch size decreasing with later laying date - there was a positive correlation between breeding success and weight dimorphism within the pair. Males showed much less seasonal weight change than females, but females of light and short-winged males laid eggs earlier than those with larger males.

Although a potentially interesting example of size selection, the observed trend of later laying dates by pairs composed of lighter females and heavier males might just as well have a purely ecological explanation. It is unclear whether the weight

dimorphism was due to real "size" differences, or just reflected differences in nutritional condition, females with the most fat reserves breeding earliest. Early pair formation (such as when both mates are resident throughout the winter) enables the male to feed the female for a long time before laying, increasing her weight but decreasing his, and enabling her to lay early. But late pair formation gives less time for such weight dimorphism to arise from courtship feeding and also results in late laying. Therefore, future studies should include other "size" measures than weight.

8.3. Sexual selection theory

It has been suggested that the reversed sexual size dimorphism in birds of prey may be caused by Darwinian sexual selection, similar to, but reversed in relation to that held to be responsible for the "normal sexual size dimorphism". The argument is that because males invest so much in breeding by supplying most of the food, competent males are a scarce, valuable resource, over which females compete, driving female size increase by intrasexual selection (Olsen and Olsen 1984; Newton 1986, p. 326). Mating preference, females choosing small males by their superior ability of providing food, might help increase dimorphism by intersexual selection (Cade 1982, p. 43; Safina 1984).

But I think sexual selection alone cannot explain the origin of reversed dimorphism at any of the three levels in figure 3; (A) why there is a role division in the first place, (B) why the direction of role division and size dimorphism is as observed, or (C) why there are interspecific differences in degree of dimorphism. A sexual selection explanation at level C would require systematic differences between species in the variance of male competence, or in the degree to which males invest in breeding, by food provisioning, such that both variables increase with increasing proportion of agile prey in the diet. Then the intensity of sexual selection might vary accordingly to give various degrees of dimorphism. But owls seem to be a remarkably uniform group in all relative roles of the sexes in parental care (Mueller 1986, p. 402), reducing the likelihood of this possibility.

9. HUNTING MODE

Most forest owls hunt from a perch, using a "sit-and-wait" - or "perch-and-pounce" - hunting technique (figs 4 and 5). But search for prey may be done in flight to some extent, as in the open-country owl *Asio flammeus*, and short hovering bouts do also occur occasionally among forest owls. Since hovering flight is the most energy-demanding type



Figure 4. - Like most forest owls, *Aegolius funereus* uses a "perch-and-pounce" hunting technique. This female is preparing for strike, showing intent attention towards the prey. Wild owl photographed in the field in SW Sweden on June 18, 1968. - Photo: R. Åke Norberg.

Figure 5. - Female *Aegolius funereus* striking a laboratory mouse released near the owl's nest in SW Sweden on June 14, 1968. The anteriormost primary wing feathers separate, exposing secondary leading edges to the air flow. But like the anteriormost primary feather, the exposed leading-edge portions of the next two feathers also have the comb-like, or serrated, structure that reduces aerodynamic noise. - From R. Å Norberg (1970, p. 59). Photo: R. Åke Norberg.



of locomotion, and since the ratio between the power needed to hover and the power available decreases with increasing mass of the bird, hovering can be expected to be less common among large than among small owls. Indeed, even the smallest owls probably exceed the critical mass below which continuous hovering can be sustained; hovering therefore probably incurs an oxygen debt in owls.

All owls use the eyes as well as the ears for prey detection and localization, but the relative importance of these senses varies among species. Specialization on one sense or the other opens up various possibilities for habitat selection and also dictates the range of hunting modes that can be used. But it also sets constraints to the types of habitat that can be efficiently exploited and to the ways prey can be efficiently searched for, involving the length of flight between perches, the height of perch, and the giving-up time before moving to a new perch (R. Å. Norberg 1970; Andersson 1981).

Visual search for prey requires a sparse forest and not too dense ground vegetation, which would conceal prey animals. Species hunting predominantly by eye usually select high vantage points from where they can search a reasonably large ground area for prey. *Surnia ulula* is a good representative of this category; it usually sits on top of trees, snags etc. and often detects prey animals at ranges far too long for acoustical detection. See also comments on *Surnia ulula* in the section: "2. Distribution of northern forest owls".

For an owl hunting in dense forest, trees and shrubs obscure much of the ground, so that a very small ground area is visible from a perch (R. Å. Norberg in preparation). This applies also when there is a dense ground cover. Under such circumstances the owl may do better by switching from using vision into relying predominantly on hearing for prey finding. But hunting by ear requires that the owl be close to the source of sound to increase its probabilities of detecting it, necessitating choice of very low perches. This worsens the prospects for visual detection, so in dense vegetation the hunting mode is dictated by what best governs auditory localization.

Aegolius funereus is a typical exponent of this hunting technique. It often hunts in very dense forest and even within thickets. And it selects very low perches, sometimes even sitting on stumps and tussocks. While following hunting owls during light summer nights in the Swedish Lapland, I recorded an average perch height of 1.7 m, an average flight length between perches of 17 m, and an average giving-up time at the perch of less than 2 min (R. Å. Norberg 1970).

Among the prey capture attempts that I witnessed, the following one illustrates how the owl's search tactic was influenced by its knowledge of where there was a prey. The vole population had crashed earlier

in spring, so prey was very scarce. I saw an owl strike at a prey, but missing it. It then flew back to the same branch from where it struck and remained there for 27 min - an unusually long time at a perch - often looking at the place where the prey had been. I made no further observations at this site, but had seen the owl on exactly the same perch once earlier the same night and once the night before. Several other perches were also used several times by the owl, in the same as well as in successive nights (R. Å. Norberg 1970).

I have also seen foraging *Aegolius funereus* and *Strix nebulosa* making long commuting flights between favourite hunting parts of their hunting territory.

From such observations, I think that owls foraging in a hunting territory know fairly well from prior experience - by sightings and auditory cues - where prey animals are. Their search behaviour in a familiar hunting territory therefore is probably guided by the conditional probabilities of prey detection, following upon knowledge of the approximate locations of prey. This must be borne in mind when testing theories of optimal search behaviour on owls, because most such theories depend on random prey distribution and assume no prior knowledge by the predator about prey location.

Most predators have a repertoire of search modes, each of which may be characterized by its search efficiency and the associated energy cost of locomotion. And the link is probably such that the most efficient search modes are also the most energy-consuming ones, whereas the ones cheapest in energy are also the least efficient. Otherwise there would not be a repertoire, but the predator would of course use the most efficient mode if it were also cheapest in energy costs for locomotion (R. Å. Norberg 1977).

An interesting question is how the choice between various search modes is affected by food availability. This has been explored by R. Å. Norberg (1977), using a mathematical model. The resulting prediction is that when prey is abundant, a predator should use high-cost and high-reward search methods, while at low prey densities low-cost and low-reward methods should instead be used. So, as prey density declines, a predator should shift to progressively less energy-consuming search modes even though they are associated with low search efficiencies.

With owls, this means that as prey density declines, owls should shift from frequent hovering, much flight, and short giving-up times at perches into search modes with less flying and longer giving-up times at perches, i. e. to less energy consuming locomotor patterns despite their lower efficiencies in prey-finding.

Similar results were obtained by Andersson (1981), using a different model based on probabilities

of prey encounter. It also treated optimal search heights.

Most owls are "searchers" in the sense that an overwhelmingly large proportion of their foraging time goes to search for prey, as opposed to pursuit and capture, which take far less time. Therefore owls cannot afford to refrain from catching a reasonably suitable prey, once detected, and so should be generalized in their diet. This is, admittedly, a vague statement, but may be taken as a generalization for most owls in a relative sense, as compared with other types of predators.

But even among owls themselves there are differences, some species definitely being more specialized than others. To mention but a few, the *Bubo* species and *Strix aluco* are generalized, with very wide diets, whereas *Strix nebulosa*, *Aegolius funereus* and *Asio otus* are more specialized, with narrower diets.

Very few tests of optimal foraging theory have been done with owls.

10. EYES AND VISION

Owls have very large eyes, surrounded by a sclerotic eye ring. It is formed by several small bony plates, forming a tube that widens backwards toward the retina. Because of this tubular eye ring the eyes have an extremely limited movability, amounting to about 1° only (Steinbach and Money 1973); for all practical purposes they may be regarded as immovable. Instead the owl turns its head for any change in direction of view.

The eyes are more forwardly directed in owls than in other birds. The left and right eyes therefore have largely overlapping visual fields, the binocular field width being 48° in *Strix aluco* (Martin 1986, p. 270). This is a prerequisite for instantaneous stereoscopic vision (as opposed to comparisons of successive views from different positions). But in owls, as in all other birds, the optic nerve from each eye crosses completely over to the diagonally opposite side of the brain (Hirschberger 1967).

In humans there is only a partial crossing over of the optic nerves, some of the optic nerve fibers going to the brain on the same side as the eye. Neural information from both eyes therefore reaches the same brain center, which permits the brain to compare the slightly different images of the same object, as seen from the slightly different angles of the two eyes. This makes depth perception possible.

But despite the complete crossing over of the optic nerves in owls, stereoscopic vision has been achieved via a different neural route than in man; it has recently been discovered that in owls there is instead a partial crossing over of nerves between optic brain centres, half of the fibers to the "visual Wulst" carrying information from one eye, the other half relaying information from the other eye (Karten et al. 1973; Pettigrew 1979).

Turning now to night vision, northern owls are not subjected to darker nights than are tropical owls. A snow cover drastically increases the light levels by night. And with overcast skies, light is reflected repeatedly between the snow and the cloud base, resulting in fairly light winter nights at high latitudes. When there is no snow, moonless nights with cloud in autumn are no darker at high latitudes than in the tropics. So the selection pressure for good vision at low light levels should be about the same regardless of latitude.

But forest owls experience much lower night-time luminance levels than do open-country owls. So it is among the most nocturnal owls, most restricted to foraging under a closed tree canopy, that evolution should have resulted in the best dark vision among owls.

The early realization 120 years ago that the many rod photoreceptors in the retina of owls are linked to the high sensitivity of the owl eye was part of the original evidence of the duplicity theory of vision, based on rod and cone photoreceptors (Schultze 1867; Martin 1986, p. 267). It has later been shown that at least some owls possess colour vision (Martin 1974).

As to vision in poor light, there are great differences between owl species. In *Strix aluco*, a strictly nocturnal owl, both absolute visual sensitivity and maximum spatial resolution at low light levels are close to the theoretical limit dictated principally by the quantal nature of light and the physiological limitations on the structure of vertebrate eyes (Martin 1986). But early claims that owl eyes are between 10 and 100 times more sensitive than the human eye to light in the human visual spectrum have been proved wrong. The same applies to the old suggestion that owl eyes might detect infra-red radiation (Martin 1986).

Recent analyses have shown that *Strix aluco* has an absolute visual sensitivity about 2.5 that of man, a more modest value. And what is more, this difference is within the normal five-fold range of absolute visual sensitivity in the human population. So there could be individual human subjects with better visual sensitivity than individual *S. aluco*. But the absolute visual sensitivity is 100 times higher in *S. aluco* than in the pigeon, *Columba livia* (Martin 1977; 1986, p. 268).

The difference in absolute visual sensitivity of the human and owl eyes can be accounted for by differences in the light-gathering power of the eyes. The minimum *f*-number (at the largest pupil diameter) is 1.3 in *S. aluco* and 2.1 in man, corresponding to a retinal illumination 2.6 times brighter in the owl than in man (Martin 1977). The value 2.6 comes from the ratio of the inverted *f*-numbers squared; $(1/1.3)^2/(1/2.1)^2$.

The *f*-number is the ratio between the focal length (approximately the distance from the front of the eye to the eye's focal plane) and the largest

entrance aperture (pupil) diameter. A camera lens with an *f*-number of 1.3 is regarded to be extremely bright (or fast, in photographic terms).

There is one more myth about owls to be removed, namely their supposedly poor vision in bright daylight. Owls see perfectly well at high, day-time, light levels (Martin 1986, p. 270), and northern owls, more than others, depend on good vision in bright light. Even some of the most nocturnal among all owls, such as *Strix uralensis* and *Aegolius funereus*, occur beyond the arctic circle where hunting must be done in full daylight throughout summer.

11. THE FUNCTION OF EAR ASYMMETRY IN OWLS - "ONE OF THOSE ENIGMAS IN ZOÖLOGY NOT TO BE SOLVED THROUGH THE RESEARCHES OF MAN"

11.1. History

As far as I know, the first time that the ear asymmetry in owls was mentioned in the literature is Street's note in 1870, in which he very briefly described the skull of an owl which he thought was of *Nyctale acadica* (now *Aegolius academicus*). He presented no illustration of it. After his brief description, Streets (1870, p. 73) made the following cautious remark: "If there had been but a single specimen of this cranium I would have been led to regard this instance of symmetry as abnormal; but as the same peculiarity of structure is presented by two (these being the only representatives of the species in the collection), it would rather suggest itself as a normal condition, although instances of coincidence of abnormality exist..." It is understandable that the remarkable asymmetry of the skull of *Aegolius* caused considerable confusion (figs 6 and 7).

The next mention of ear asymmetry in owls is Collett's paper from 1871 which contains the first published illustration of asymmetrical ears in owls; the asymmetrical skull of *Aegolius funereus*. A very similar illustration appeared in the Norwegian version of this paper (Collett, 1872) and is reproduced as my figure 6. Collett made his observation independently of Street (1870), to whom he referred in a note added later. At the time Collett submitted his 1871 paper, the journal containing Streets 1870 article had probably not reached Europe according to an editorial note, "in justice to Herr Collett".

Collett put high confidence in his observations and expressed no hesitation in regarding this asymmetry, and those in other European owls (Collett 1881), as typical for the respective species. Collett made many original observations on ear asymmetry that have been overlooked in later studies. His two papers on owl ears, originally in Norwegian, are available also in English - for those

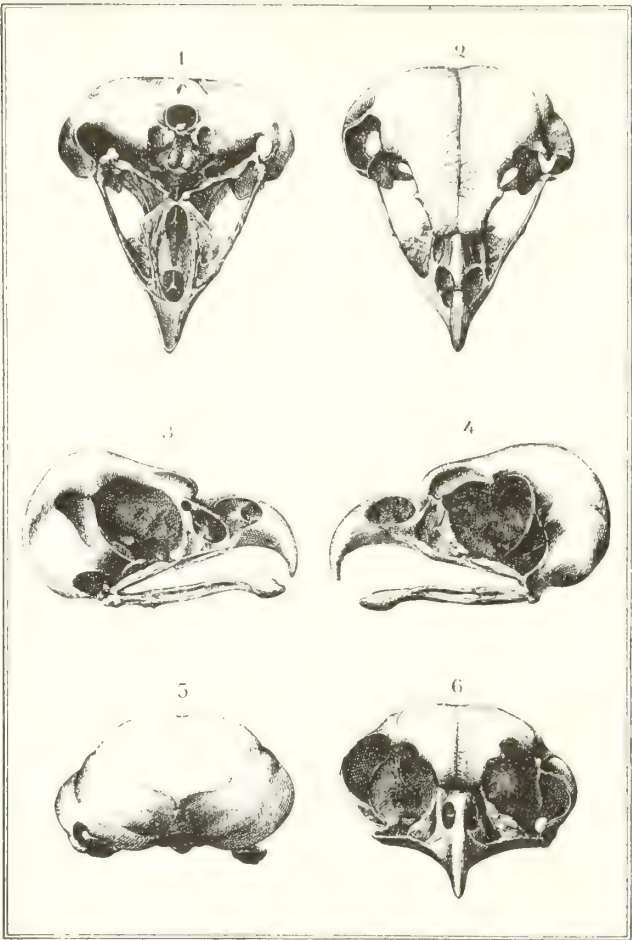
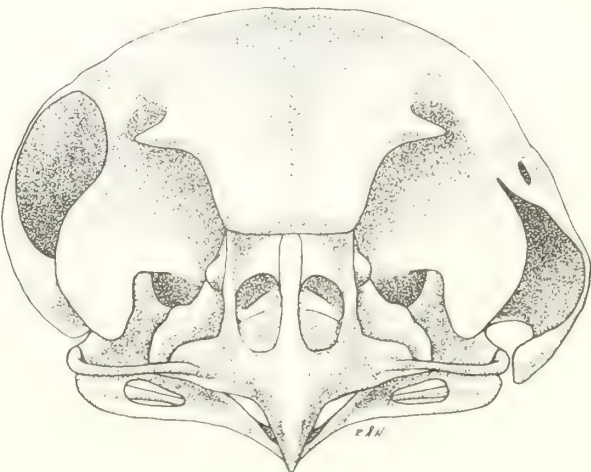
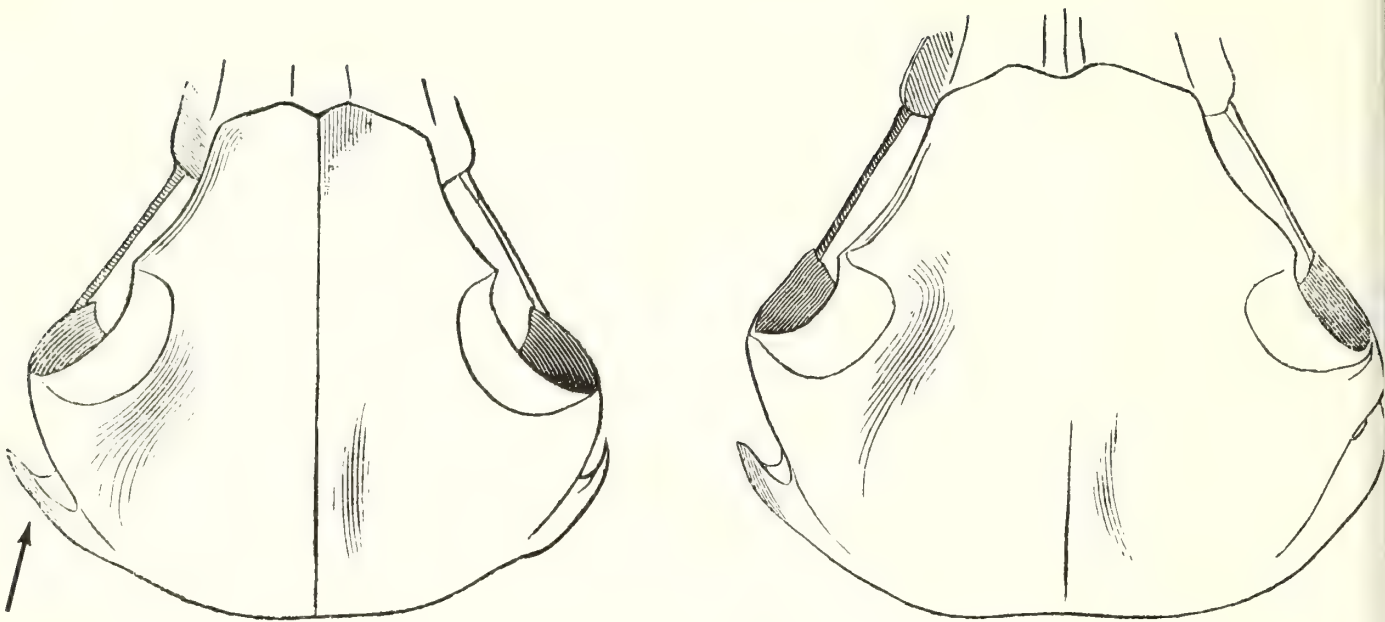


Figure 6. - The skull of *Aegolius funereus*. This illustration from Collett (1872) and a very similar one in Collett (1871) are the first published illustrations of ear asymmetry in owls.

Figure 7. - Frontal view of the skull of *Aegolius funereus*. - From R. Å. Norberg (1978, plate 8).





Figures 8 and 9. - Dorsal views of the skulls of *Strix uralensis* (8) and *Strix nebulosa* (9) showing the bilateral asymmetry of the squamoso-occipital wings, which are located lateral to the ear openings in the skull (indicated by the arrow). - Reproduced without change from woodcuts in Collett (1881, pp. 29 and 33). - The woodcut illustration technique is something to reflect upon when making today's computer-generated illustrations! This one is from a strictly scientific publication by Collett.

preferring that (Collett 1871 is an English version of his 1872 paper, and Shufeldt, assisted by his Norwegian wife, translated Collett 1882; Shufeldt 1901a, p. 120).

Collett (1881) described ear asymmetry in several European owls, and two of his 1881 illustrations appear as my figures 8 and 9. Figure 10 gives an overview of the occurrence of ear asymmetry among owls (from R. Å. Norberg 1977). It is discussed further in the section: "12. Evolution of ear asymmetry".

The bilateral ear asymmetry in owls attracted early attention and arouse curiosity about its function. Referring to the skull asymmetry in *Aegolius funereus*, Shufeldt (1901b, p. 715) wrote: "How such a condition as this asymmetry came to be evolved will probably remain one of those enigmas in zoölogy not to be solved through the researches of man. It is difficult for me to see what especial advantage it can bestow upon the bird, or how it would better fit it for the struggle for its existence."

11.2. Theories

11.2.1. Stresemann (1934)

Stresemann (1934, ppp. 133-134) seems to have been the first to associate the function of ear asymmetry in owls with directional hearing. With special reference to the asymmetry of the skull in *Aegolius*, Stresemann wrote (my translation from

German): "it would seem [dürfte] to be of importance for the localization of a sound source. During intent listening, owls usually move the head about the sagittal axis, i. e. turning one ear opening downwards, the other one upwards".

This was all that he offered in terms of explanation, but it was important, being the first time an association was made with sound localization. And the inference obviously followed naturally from Stresemann's observation of head tiltings in owls during sound localization, whereby one ear opening temporarily becomes located above the other (fig. 15) (to be discussed further below).

11.2.2. Pumphrey (1948)

The next big step towards an understanding of the ear asymmetry in owls came in 1948. From theoretical considerations, Pumphrey (1948, p. 324) formulated a theory for the horizontal and vertical localization of a sound source, using two ears. The conditions were supposed to be fulfilled by the asymmetrical ears of owls and were as follows:

"(1) The sound must be complex and the ears competent to resolve it into at least three bands of frequency in such a way that independent comparison of the signals arriving at the two ears is possible in each band.

(2) The two ears must have a direction of

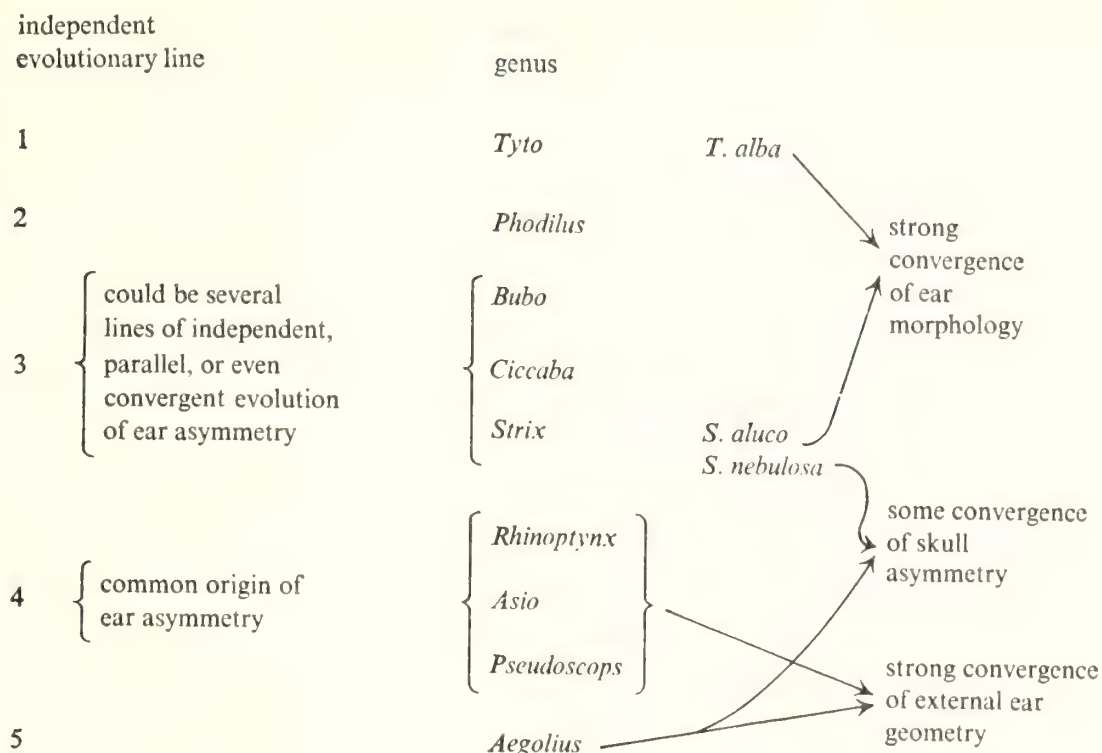


Figure 10. - Scheme summarizing the evolutionary history of ear asymmetry among owls. At least five cases of independent origin of ear asymmetry can be identified (left column). The convergence indicated for *Tyto alba* and *Strix aluco* could be extended to include more species of the genera *Tyto* and *Strix*, the ones listed being the most obvious and best known. But several *Strix* species lack any trend towards convergence in ear structure with *Tyto alba*. - From R. Å. Norberg (1977, p.402).

maximum sensitivity which is different for each band and is different for the left and right ear for at least two of these bands."

In discussing the ear asymmetry in *Asio*, Pumphrey (1948, p. 324) postulated a vertical asymmetry of the ears' directional sensitivity pattern: "...for wave lengths comparable with the slit lengths the direction of maximum sensitivity will be directed above the horizontal plane for the right ear and below it on the left." These predicted asymmetries of the directional sensitivity patterns at high frequencies were first verified by R. Å. Norberg in 1968. Payne (1971, p. 566) cited a personal communication by Pumphrey, further explaining Pumphrey's theory.

Pumphrey's (1948) theory is extremely insightful. But it is very general, and as regards the asymmetrical ears of owls it is somewhat vague. The theory given by R. Å. Norberg (1968; see below) is more precise and simpler; but it satisfies the two minimum conditions given by Pumphrey and so can be seen as a special case of Pumphrey's fairly general formulation.

11.2.3. Payne (1962)

Based upon recordings of sound intensities at

the eardrums of the barn owl, *Tyto alba*, Payne (1962, pp. 157, 159) concluded:

"Throughout the spectrum of the frequencies audible to the Barn Owl, one area surrounding the line of sight will always receive sounds at maximum intensity." "... all features [of the directional sensitivity diagrams] in the right ear occur about 10 to 15 degrees higher than their mirror image complements for the left ear. This is undoubtedly linked with the asymmetry of the ears. ... My theory, then, puts only one demand on the owl, namely, that it orient the head in such a way as to hear all frequencies, audible to it in a complex sound, at maximum intensity in both ears. When it has achieved such an orientation, it will automatically be facing the source of the sound..."

This theory has not been supported by later work. But in 1971 Payne suggested a modified version, which is more similar to that of R. Å. Norberg (1968; see below).

11.2.4. Norberg (1968); "The Pumphrey-Norberg theory"

As late as in 1968, 67 years after Shufeldt's remarks in 1901 (Shufeldt 1901b, p. 715; see above:

"11.1. History"), the problem still remained of giving a functional interpretation of the ear asymmetry in owls, as highlighted by the following statement by Schwartzkopff (1968, p. 45): "The difficulties of combining morphological and ecological data with physiological findings are illustrated most clearly by the almost historical problem of explaining the asymmetry of the external ear in some owls".

In 1968 I presented a complete, but simple, theory on the principles of the function of the morphological asymmetry of owl ears (R. Å. Norberg 1968). It was based on data from acoustical measurements on a model head, using a skull of *Aegolius funereus*, with soft plastic material replacing soft anatomy parts, covered by a natural skin with feathers, and with 6.3 mm diameter microphones replacing the eardrums.

The theory states that an owl with asymmetrical external ears can localize the direction of a sound source binaurally both in the horizontal plane (in azimuth) and in the vertical plane (in elevation), simultaneously, and with the same accuracy, without an additional judgement after turning the head about its longitudinal axis. A condition is that the sound contains low as well as high frequency components. And rustling sounds made by prey moving in snow as well as in vegetation, fresh or dry, do cover a wide frequency spectrum, therefore fully satisfying this requirement (R. Å. Norberg 1968, p. 201).

The principles of directional localization with asymmetrical ears are as follows (from R. Å. Norberg 1968) (see figs 11-14):

Horizontal, or azimuth, determination :

1. By comparison of the times of arrival of sound at the two eardrums, i.e. by measuring interaural time differences by binaural comparison.

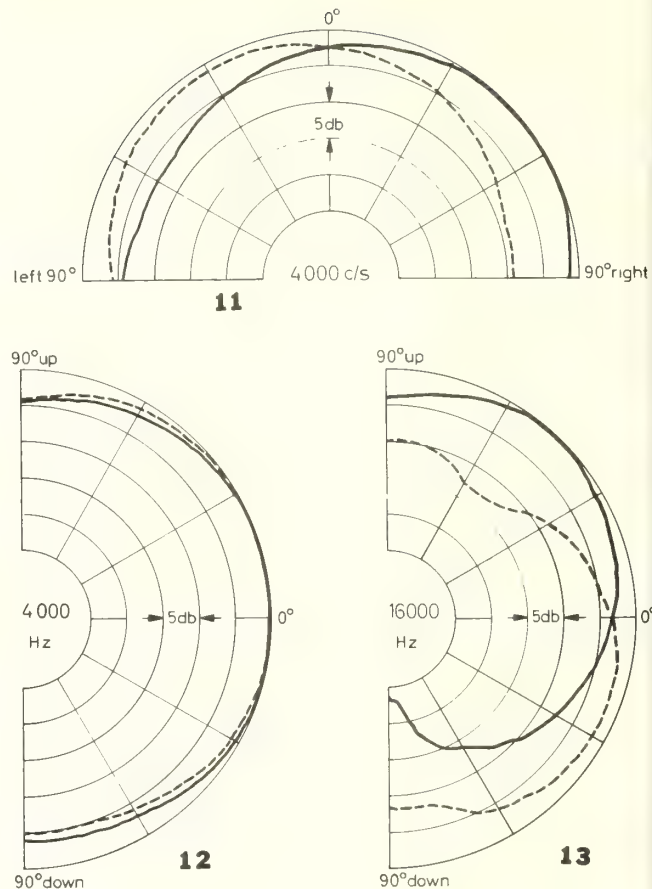
2. By comparison of the intensities in the two ears of low-frequency components of the sound, i.e. by measuring interaural intensity differences by binaural comparison.

For sounds of low frequencies, with wave-lengths longer than the dimensions of the head, the morphological asymmetry does not affect the directional sensitivity pattern of the ears. For such low frequencies, the ears therefore function like symmetrical ears, providing time and intensity cues for horizontal localization in the usual way, as described above under point 1 and 2 (figs 11, 12, and 14).

Vertical, or elevation, determination :

3. By comparison of the intensities in the two ears of high-frequency components of the sound, i.e. by measuring interaural intensity differences by binaural comparison.

This is identical to point 2 above, except that it is for high frequency sound components, whose wave-lengths are about equal to, or shorter than, the dimensions of the ear opening and head. For such



Figures 11, 12, and 13. - Relative sound pressure levels at the left (-----) and right (-----) eardrums in *Aegolius funereus*, measured on a model head built on a skull, covered with skin and feathers, and with soft plastic material replacing soft anatomy parts. The upper diagram is for directions of incidence of sound in front of the owl and in the horizontal plane of the head. Comparison of intensities in the left and right ear enables the owl to localize a sound source in the horizontal plane, using low frequency components of the sound. - The diagram at lower left is for directions of incidence of sound in front of the owl but in the vertical plane of the head. The structural asymmetry of the ears has no effect on their directional sensitivity at low frequencies. Therefore, the ears are functionally symmetrical at low frequencies, and provide no cues to vertical localization. - The diagram at lower right is also for directions of incidence in the vertical plane of the head. But at high frequencies the structural asymmetry of the ears strongly influences their directional sensitivity. Comparison of intensities in the left and right ear enables the owl to localize a sound source in the vertical plane, using high frequency components of the sound. This is an important function of ear asymmetry. - From R. Å. Norberg (1968, pp. 193, 196).

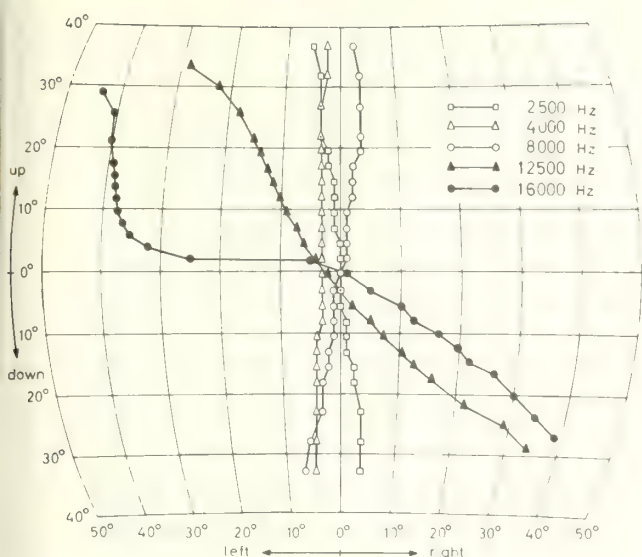


Figure 14. - Projection of the space in front of the owl (*Aegolius funereus*). The curves show from which directions of incidence a sound is equally loud in both ears for various frequencies. These are important reference directions; the horizontal direction of a sound source can be judged with reference to the vertical, equal-sensitivity, curves for low frequencies, and the vertical direction can be judged with reference to the oblique, equal-sensitivity, curves for high frequencies. - From R. Å. Norberg (1968, p. 197). Later measurements on intact heads, using a probe tube microphone, showed vertical asymmetries also at somewhat lower frequencies, at 8000 Hz and 10 000 Hz, and to a lesser extent at 6300 Hz (R. Å. Norberg 1978, pp. 405-406).

sound, the structural asymmetry of the ears does affect the ears' directional sensitivity so that the region of maximum sensitivity is directed obliquely downwards for one ear, obliquely upwards for the other. This provides excellent cues for vertical localization via binaural intensity comparisons, just as for horizontal localization with lower frequencies, under point 2 (figs 13 and 14). The version of this theory given by R. Å. Norberg in 1978 (pp. 407-408) is identical except for the delimitation of frequency domains for azimuth and elevation determinations in *Aegolius funereus* (see legend to fig 14).

To summarize: An owl with asymmetrical ears can determine the direction of a sound source simultaneously in the horizontal and vertical planes by using (1) binaural *time* comparisons and the whole frequency spectrum for *horizontal* localization, (2) binaural *intensity* comparisons and *low* frequency components for *horizontal* localization, and (3) binaural *intensity* comparisons and *high* frequency components for *vertical* localization (figs 11-14).

This theory satisfies the two minimum

conditions given by Pumphrey (1948) and so can be seen as a special case of Pumphrey's fairly general, but insightful, formulation. I therefore follow Knudsen (1980, p. 309) and term it "*The Pumphrey-Norberg theory*".

This theory has been fully supported by behavioural and neurophysiological work made on the barn owl, *Tyto alba*, by Knudsen (1981); Knudsen, Blasdel, and Konishi (1979); and Knudsen and Konishi (1979). They have shown convincingly that barn owls do localize sound as predicted by "*The Pumphrey-Norberg theory*". But the claim by Knudsen (1980) of having devised a new theory of sound localization by the addition to my theory of an interaural time factor is absolutely wrong. It was all contained in R. Å. Norberg (1968, pp. 198, 199; and again in 1978, p. 407). For instance, in discussing horizontal localization with the aid of interaural time differences, I concluded: "The ear apertures in *Aegolius funereus* thus are set so far apart that the interaural time difference may well be of considerable importance in the owl's directional hearing." (R. Å. Norberg 1968, p. 198).

Knudsen and Konishi have made exciting neurophysiological work on owl hearing, and among other things described a neural map of auditory space in *Tyto alba* (Knudsen and Konishi, 1978). Even though different directions of incidence of sound become codified as binaural differences in time and intensity, the neural representation of the various directions is in the form of a morphological map of neurons in the brain, reflecting the auditory space outside.

11.3. Head and ear size

The longer the distance between the two ears, the larger the difference in time of arrival of a sound at the two eardrums, and the better the accuracy of localization with time cues, given a certain angle of incidence (R. Å. Norberg 1968, p. 198). And the larger the head and ears are, the more pronounced the directionality of the ears become (i.e. the larger the deviation from omnidirectionality, or equal sensitivity in all directions), and the better the accuracy of localization with intensity cues at low frequencies.

Similarly, when the ears are asymmetrical, larger head and ears means that the asymmetry affects the ears' directional sensitivity pattern already at lower frequencies than with smaller head and ears (R. Å. Norberg 1978, p. 405). And since sound of low frequencies carry longer than those of high, a big head and large facial ruffs and discs are advantageous for directional hearing. This explains why the head is so large, particularly among owls relying much on hearing for prey localization.

11.4. Sound localization with symmetrical ears

I should maybe add that it is not against the rules for an owl with perfectly symmetrical ears to localize, by ear, a concealed prey making rustling sounds, and to catch it with high precision. But in order to achieve the same accuracy in vertical localization as do owls with asymmetrical ears, it would need to make two directional judgements with an intervening tilting of the head through 90° in between, or two tiltings through 45° , in opposite directions (Figure 15). The latter seems to be the most common mode in, for instance, *Surnia ulula*.

So, the main advantage with asymmetrical ears is that the horizontal and vertical direction of a sound source can be determined simultaneously, with the same accuracy in both planes, and without head tilting. This saves time. But more importantly, it seems to be indispensable for localizing and catching hidden prey that moves; with asymmetrical ears the precise location of a moving prey can be continuously monitored. But with symmetrical ears, horizontal and vertical directions have to be determined one at a time, one after the other, with an intervening tilting of the head in between.

11.5. Head tilting in young owls with asymmetrical ears

In view of what has been said above about owls with asymmetrical ears having no need of tilting the head during sound localization, it might seem disturbing - to put it mildly - that young owls do tilt their head intensively during sound localization. And what is more, this is done particularly by species with strongly asymmetrical ears, such as *Asio otus* and *Aegolius funereus* (fig. 15).

But considering the kind of conflicting information that they receive from the two ears, it is obvious that this is part of a learning process that is necessary before they can take full advantage of their ear asymmetry (R. Å. Norberg 1973, pp. 99, 101). Look at figure 14 and consider a sound source that is located straight ahead but somewhat upwards (in the head's median, sagittal, plane but above its horizontal plane). Then the sound reaches both ears simultaneously, and low frequency components are equally loud in both ears, which indicates that the sound source is in the median plane of the head. But high frequency components are louder in the right ear, and this the owl must probably learn to interpret as a sound coming from above, not from the right. Presented with this acoustical input, we would perceive a phantom source, distributed in space, with low frequencies straight ahead, but with high frequencies to the right. The head tiltings in young owls of some species with asymmetrical ears strongly suggest that the rule for how to interpret this



Figure 15. - Young *Aegolius funereus* tilting its head through about 90° . Extensive head tiltings occur in young owls among species with asymmetrical ears - exactly the ones that would seem not to need it. This is obviously for training to interpret correctly the conflicting auditory information received from the two asymmetrical ears, as explained in the text. Once this information can be correctly used, species with asymmetrical ears can judge both the horizontal and vertical direction of a sound source at the same time, without tilting the head (provided the sound contains high as well as low frequency components). Captive owl, July 1964. - From R. Å. Norberg (1973, p. 99). Photo: R. Å. Norberg.

information correctly is not innate in these species, but has to be learnt.

Head rotation is a means of resolving this ambiguity; when the axis of rotation of the head passes through the true location of the sound source, rotation of the head does not cause any change of the binaural pattern of the sound perceived. With all other orientations it does.

But when these head rotations occur in owls - young or adult - with symmetrical ears, they are for

vertical localization, rather than for resolution of information that is hard to interpret without experience.

12. EVOLUTION OF EAR ASYMMETRY

12.1. The origin of ear asymmetry

Owls that rely much on hearing to locate prey may do so either because they select a habitat where vision is obscured by dense vegetation, or because prey is concealed among dense ground vegetation or under snow. To increase the probabilities of detecting prey by ear, the owls need to be close to the sound source. This is why those species, which hunt predominantly by ear, usually sit or fly low over the ground when searching for prey (R. Å. Norberg 1970).

When such an owl has detected a rustling sound, and starts localizing the source, the direction of the sound source usually forms a shallow angle with the ground because of the low position of the owl. Therefore, with a given angle of localization error, the same in elevation and azimuth, the "range

miss" becomes larger than the "lateral miss", i. e. the distance that the owl misses the target by striking too close or too far away with respect to the target is bigger than the lateral distance that the owl strikes to the side of the target (fig. 16) (R. Å. Norberg 1977). This is a crucial factor that calls for good vertical localization ability of all owls which rely on hearing for prey localization. It is also an important reason for the evolutionary origin of ear asymmetry among owls.

12.2. Convergent evolution of ear asymmetry

Selection pressure for improved ability of vertical localization of sound obviously lies behind the evolution of all types of bilateral ear asymmetry among owls. Various evolutionary lines have produced different structural solutions which probably represent various degrees of success (R. Å. Norberg 1977).

After careful examination and comparison of the morphology of owl ears, R. Å. Norberg (1977) concluded that ear asymmetry has evolved

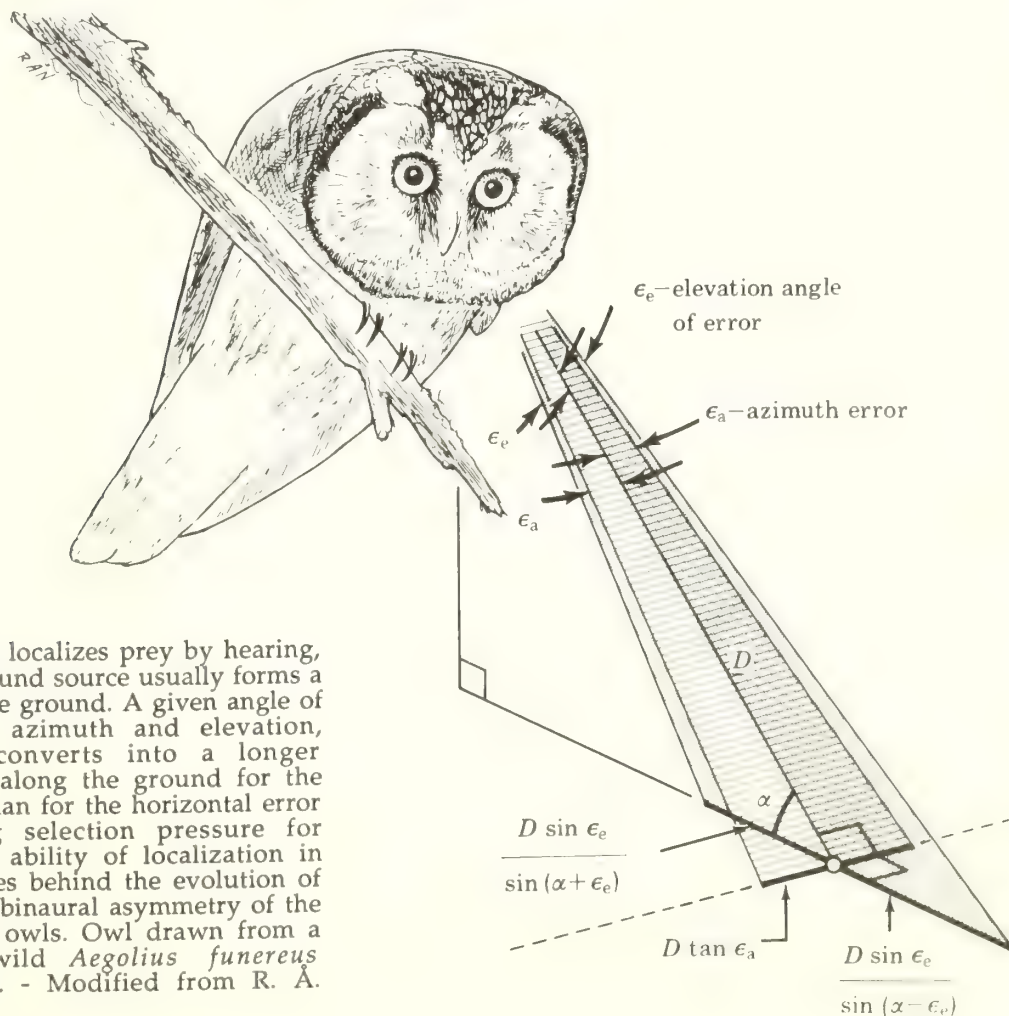


Figure 16. - When an owl localizes prey by hearing, the direction of the sound source usually forms a shallow angle with the ground. A given angle of error, the same in azimuth and elevation, therefore usually converts into a longer target-miss distance along the ground for the vertical error angle than for the horizontal error angle. The ensuing selection pressure for improvement of the ability of localization in elevation probably lies behind the evolution of all types of (vertical) binaural asymmetry of the external ears among owls. Owl drawn from a photograph of a wild *Aegolius funereus* preparing for strike. - Modified from R. Å. Norberg (1977, p. 401).

independently in at least five evolutionary lines among owls. The generic representation appears in figure 10.

The presence of a snow cover during a large part of the year at high latitudes is probably one reason why such a large proportion of the northern forest owls have asymmetrical ears (41% of the species; see above: "2. Distribution of northern forest owls; 2.2. Conclusion"). This relationship probably came about in two ways; (1) the evolution of ear asymmetry probably took place at high latitudes within some of the phyletic lines that ever produced it, governed by strong selection for improved abilities of auditory localization of prey under a snow cover; and (2) species that have evolved ear asymmetry elsewhere can more easily invade northern latitudes than can species with symmetrical ears.

The analysis of ear structure among owls also led to a firm rejection of the former systematic subdivision of the Family Strigidae into the subfamilies Buboninae and Striginae. The subfamily Striginae was erected by Peters (1940) to accommodate owls with big heads and large ears, thought to represent one monophyletic group. But these owls have a mixed phylogenetic origin, as revealed among other things by the morphology of their ears (R. Å. Norberg 1977).

13. OWLS AND PREY CYCLES

In the ecological context, most owls are closely associated with small mammals, in particular with small rodents. Predator-prey interactions play an important role in the regulation of population densities of both owls and small mammals, even though the mechanisms are intricate.

The dramatic cyclic population fluctuations among mice, voles, and lemmings at high latitudes are one of the most fascinating phenomena in ecology (figs 17-20). The famous population cycles of small rodents are a classic problem in population ecology. Small rodent predators, including owls, track the fluctuations of their prey. But the rodent cycles are not simply driven by predators, even though predators definitely interact with prey numbers. Various explanations of the rodent cycles and the mass-irruptions have been much debated through times.

Let us focus on the Norway lemming, *Lemmus lemmus*, which is a well-known, but extreme, example of a cyclically fluctuating vole. It has a very restricted distribution in alpine regions in Norway, Sweden, Finland, and on the Kola peninsula, where it occurs in the alpine birch forest and the lower parts of the alpine heath. Its cyclic mass occurrence,



Figure 17. - The first known illustration of lemmings. Woodcut from 1555 showing Norway lemmings, *Lemmus lemmus*, falling with the rain, reflecting the then prevailing view of the origin of their mass-occurrence in "lemming years". The group of lemmings at lower left probably symbolizes an irruptive movement, and predation on lemmings is shown to the right. - From Olaus Magnus (1555; reprinted 1976, Vol. 4, p. 60).



Figure 18. - Detail of woodcut from 1555 showing an eagle owl, *Bubo bubo*, preying on hares and another owl taking a rodent. - From Olaus Magnus (1555; reprinted 1976, Vol. 4, p. 156).



Figure 19. - An artist's representation of an irruption of Norway lemmings, *Lemmus lemmus* at the turn of the last century. - Based on Brehm; From Jägerskiöld, Lönnberg, and Adlerz (1903, p. 9).

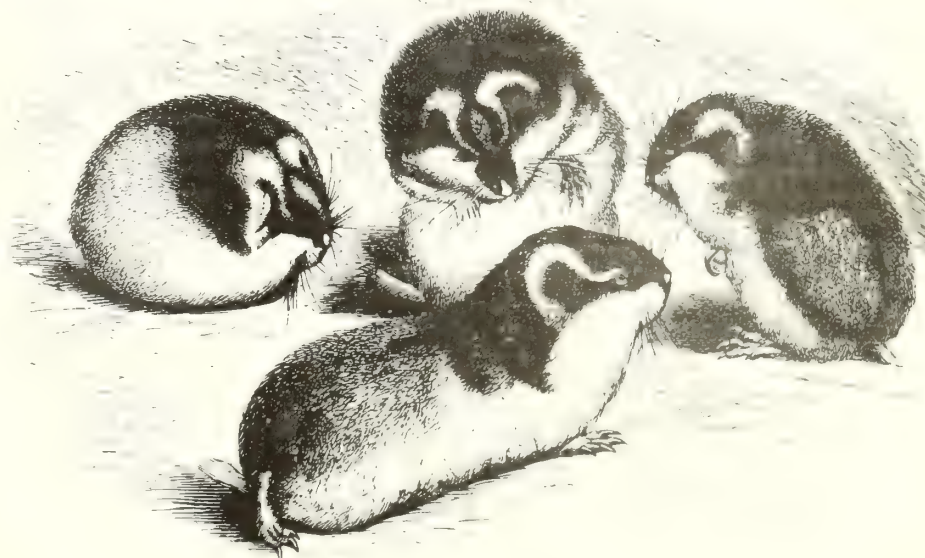


Figure 20. - *Lemmus lemmus* in close view. - From Brehm (1922, Vol. 11, p. 259).

sometimes followed by large-scale irruptions, which take it far beyond its ordinary distribution range, have caused much speculation and many misconceptions.

In "History of the Scandinavian People" from 1555, Olaus Magnus made an early attempt (430 years ago) at explaining where lemmings came from when they suddenly, and enigmatically, appeared in enormous numbers in areas where they did not normally occur (my translation from Swedish): "During rainstorms and sudden showers it sometimes happens that small quadrupeds, called 'lemmar' [lemmings], the size of voles and with mottled fur, fall down from the sky. It is not known from where they come, whether they originate from remote islands and have been carried here by winds, or if they have simply [sic!] been produced by fertile clouds and thence arrived to the ground. It is true, however, that soon after they have fallen to the ground one can find still undigested herbs in their bowels." Olaus Magnus also presented the earliest known illustration of a lemming, in the form of a woodcut (fig. 17). It shows lemmings falling with the rain, but also a group of lemmings, probably symbolizing their mass-movements, as well as carnivores preying upon them (see also figure 18).

A much more recent misconception about the exodus of lemmings in peak population years is the view that their movement away from an overcrowded area, leading to most of the irruptive animals dying from starvation, predation, or by drowning, is a bizarre altruistic mass-suicide, "for the survival of the species", which leaves the few remaining animals to survive when competition for food has thus been relaxed. Such group selection, "for the good of the species", arguments must be replaced by explanations based on individual selection (Williams 1966; Dawkins 1976).

The small rodent fluctuations are periodic with an average of about four years between population peak years, but shorter and longer intervals do sometimes occur. Similar population cycles occur also in the snow-shoe hare, *Lepus americanus*, and among its main predators. But this famous wildlife population cycle is about 10 years long, a result of the lower reproduction potential of the hares as compared with voles and lemmings.

There is a very clear geographic trend for cyclic population fluctuations among small mammals; the farther to the north they exist the more common the fluctuations become and the larger their amplitudes (but the periodicity is still about four years) (Hansson and Henttonen 1985).

The reasons for the cyclicity and the migratory outbreaks, and the mechanisms involved, are still not fully understood. There obviously are interactions at four levels; between the soil, the vegetation, the rodents, and the predators. And time delays, cyclic phenotypic and genotypic changes of the

plants and rodents, as well as behavioural changes in rodents, are also involved (Krebs et al. 1973). Parasites and diseases may also play a role.

A simplified view of the process is as follows. After a population minimum, when populations of plants, rodents, and predators have all crashed (or the plant quality as food has deteriorated), the vegetation starts to recover, followed by an increase in rodent number. Predators eventually increase in number also, but because of the necessary time delay, and their lower reproduction potential as compared with rodents, they cannot match the rodents' rate of increase and therefore cannot regulate rodent density until rodent numbers approach a ceiling, set by vegetation.

The growth of plants may eventually be retarded owing to depletion of nutrients in the soil. And an ultimate limit to plant density is set anyway by packing constraints (R. Å. Norberg, in press). Therefore, rodents eventually overexploit the vegetation, whereupon the rodent population crashes. The predators, having by now reached high population densities, may still survive for some time by switching partly to alternative prey. But they are destined eventually to decline heavily in number, by starvation and emigration.

When the population density of small mammals increases, their predators may respond in two ways; by switching to eating more rodents (functional response) and by increasing in density by reproduction or immigration (numerical response). Predators are likely to have the following five effects on small rodent cycles and on the population fluctuations of other prey animals.

(1) Predators retard the population increase of their small rodent prey, thus tending to lengthen the cycle.

(2) When small rodents are reaching high population densities, many predators that normally eat mainly other prey do switch over to eating rodents, which are easy prey, leaving their normal prey species to increase in numbers. Their population densities therefore tend to increase in synchrony with that of rodents, but with some time delay.

(3) Because predators switch over partly to other prey during the rodent decline phase, they survive for some time despite the rodent decline and so can continue to reduce the densities of the small rodent populations until they reach much lower levels than would have been attained without predators. This is possible because when rodent density has started to decline (primarily for other reasons than predation), the density of rodents becomes progressively lower in relation to predator density. This is in striking contrast to the increase phase, when the strong numerical dominance of rodents, together with their then high rate of increase, led to runaway population growth, inaccessible to predator control.

(4) After predators have switched partly to alternative prey, they cause a population decline among these prey also; it occurs somewhat after the time of the rodent population crash, but clearly synchronized with it. Predators should be more able now than at other times to exert population control over other prey, because the previously high densities of small rodents have enabled the predators to build up higher population densities than they could have done without the rodent outbreak.

(5) Predators are likely to emigrate to new areas during their peak and decline phases, and they therefore tend to synchronize population fluctuations of their prey (small rodents as well as others) over large areas, the population minimum of small rodents in the source area being the synchronization set point. But time delays, owing to the time elapsed before emigration starts and for predation to reduce prey densities in the target areas, lead to a phase displacement between areas.

When the predators involved are specialized on small rodents as food, and cannot survive for long on alternative prey, the predators have a destabilizing effect on their prey as just described, tending to increase the amplitude of the population fluctuations in rodents.

But when the predators are more generalized, being able to survive entirely on other prey than small rodents, they remain at fairly high densities even after small rodent populations have crashed. Such predators are therefore always present at high enough densities to be able to control the density of small rodents when they start to increase. Further south, other potential prey species than small rodents are usually commoner than at high latitudes. This favours generalized predators, and this is probably the main explanation why the population cycles of small rodents are much less there than at high latitudes (Erlinge et al. 1983; Hansson and Henttonen 1985).

To summarize, predators specialized on small rodents as food tend to destabilize the rodent cycles, whereas generalized predators tend to have a stabilizing effect, sometimes to the extent that cyclic fluctuations are suppressed altogether among small rodents. And specialized as well as generalized predators both tend to synchronize population fluctuations of small rodents and alternative prey, both locally and over larger areas. The time of the rodent population minimum is the synchronization set point, i. e. when the phase-lock is achieved. The larger mobility that predators have, the larger the area over which they may synchronize population fluctuations among their prey. So, owls and diurnal birds of prey have larger potential for effecting large-scale geographic synchronization of prey cycles than have carnivorous mammals with their lower mobility.

In 1941 Stig Wesslén, a Swedish wildlife

photographer and writer, vividly described how owls and raptors, occurring at extremely high densities, switched over to alternative prey after a population crash of *Lemmus lemmus* and other small rodents in early summer in Swedish Lapland; and different predator species even turned to eating each other under the prevailing, desperate, starvation conditions. This continued until the whole predator population was completely wiped out due to nest desertion, starvation, predation, and emigration. Wesslén (1941, pp. 145-159) clearly recognized that predators effected a synchronization of population fluctuations of small rodents and of alternative prey animals, such as hares, ptarmigans, grouse, ducks, shorebirds, and passerines.

Yngvar Hagen (1952, pp. 583-588) made similar observations of different predator species eating each other after a small rodent crash in Norway. He also provided data on the strict synchronization between population fluctuations of small rodents and game birds, *Lagopus*, and attributed this to predators, as outlined above (my points (2) and (4)). Later studies confirm a synchronization effect by predators across prey species (Hansson 1984; Henttonen 1985; Järvinen 1985).

To gain a thorough understanding of the interactions between populations of predators and prey, and the effects that predators have on the regulation of prey population density, studies should be conducted on the collective populations of all essential species of prey as well as of predators. Examples of such large-scale ecological studies on small rodents and their predators, including owls, are the classical work by Craighead and Craighead (1956) and a more recent study by Erlinge et al. (1983). Both show that predation has a regulatory effect on small rodent populations.

Northern owls are very flexible in the number of eggs they lay in a clutch; they can markedly increase or decrease clutch-size in immediate reaction to available food-supply (figs 21 and 22). In areas where the prey populations undergo marked fluctuations the owls do even refrain from breeding in bad years.

In areas where small rodents are strongly cyclic, the owls that are most specialized on small rodents tend to be nomadic - such as *Asio otus* and *Asio flammeus* - whereas species with a generalized diet show site tenacity - such as *Strix uralensis* and *Strix aluco* (Myserud 1970; Lundberg 1979; Sonerud 1986). Still others may show a mixed strategy, females tending to be more nomadic than males, which seems to be the case in *Aegolius funereus* (Lundberg 1979; Wallin and Andersson 1981; Löfgren, Hörnfeldt, and Carlsson 1986; Korpimäki, Lagerström, and Saurola 1987).

When there is low correlation from place to place in food fluctuations, nomadism is obviously advantageous for predators that are strictly specialized on cyclic prey (Andersson 1980). And



Figure 21. - Example of a supply of surplus prey in an owl nest in a year when prey is abundant. This is from a late nest of *Aegolius funereus* in SW Sweden (at Kelles) on May 20, 1973, when the first egg was just laid. There was no egg on May 19, so the prey represent "courtship feeding" prior to egg-laying. The 18 prey animals are (from top left to bottom right): 2 *Microtus agrestis*, 2 *Clethrionomys glareolus*, 1 bird nestling, 12 *Sorex araneus*, and 1 *Sorex minutus*. Their combined weight was 191 g. Of these 18 prey only one *Sorex araneus* remained in the nest on May 22. The female eventually laid 7 eggs, which is unusually many; 6 eggs hatched and 5 young fledged. - Photo: R. Åke Norberg.

when a rodent population crash has hit an area at high latitudes, migration southward should be advantageous for rodent predators even if rodent cycles were synchronized and in phase over large areas. This is because a rodent crash at high latitudes often results in extremely low rodent densities, probably much lower than further south where there is less cyclicity, or none at all.

Differences in yearly, winter, migration patterns between northern owls are affected by prey availability as determined by choice of hunting habitat, hunting mode, and visual and auditory prey localization abilities (Sonerud 1986).

The regular and violent population fluctuations among small mammals and their predators at high latitudes may allow higher evolutionary rates than would otherwise be possible. This is further explained at the end of the next section: "14. Adaptations among northern forest owls".

14. ADAPTATIONS AMONG NORTHERN FOREST OWLS

The most conspicuous adaptation among owls to the cold northern climate is the dense feathering, in

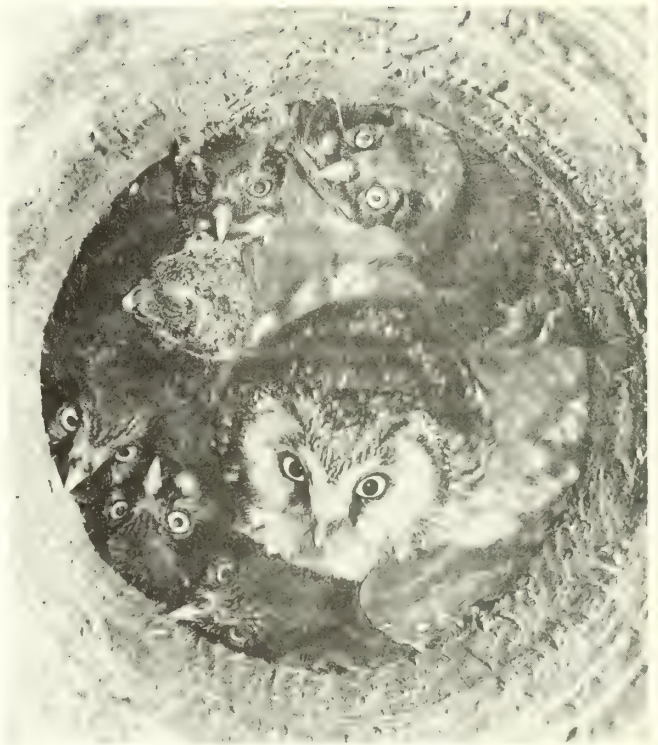


Figure 22. - Female *Aegolius funereus* in another nest in SW Sweden (at Flottatjärn) with 6 young on May 4, 1973. All 6 fledged. This was another large brood in a year with high food abundance. - Photo: R. Åke Norberg.

particular around the bill and on the legs and toes. For example, the northern fish owl *Ketupa blakistoni* differs from the other, more southern, fish owls in having feathered tarsi (Fogden 1973). And in the northern part of its range, the collared scops owl, *Otus bakkamoena*, has dense plumage on its tarsi and in Japan and China even the toes are well feathered (Hekstra 1973, p. 103).

Another plumage characteristic is the predominance of grey colour among northern owls, which may be a thermoregulatory adaptation (see above: "3. Colour morphism").

Ear asymmetry occurs in a much larger proportion of the species among northern owls than among tropical ones. A reason is that the occurrence of a snow cover during much of the year should select strongly for ear asymmetry, probably leading to its evolution at high latitudes, but also favouring invasion of species who evolved ear asymmetry elsewhere.

The rationale for this is as follows. A snow cover drastically damps the rustling sounds made by prey moving in tunnels in the snow or in the subnivean space. Owls attempting to detect such sounds therefore need to be close to the sound source, and so should select low perches or fly low

over the ground if searching for prey in flight. When sounds are detected from low heights, the directions of the sound sources form shallow angles with the ground. This tends to result in large localization errors in elevation, which in turn result in "range misses" - the owl striking too close or too far away with respect to the target. Vertical asymmetry of the external ears reduces this elevational error and the associated range miss. And this is the reason for the evolutionary origin of ear asymmetry among owls (see section: "12. Evolution of ear asymmetry").

Small mammals living beneath the snow are difficult to detect and localize. Plunge-holes in the snow, such as those shown in figure 25, are striking evidence (no pun intended) of the efficacy of the asymmetrical ears in owls. It should be noted, however, that some rodents, in particular *Microtus* species, frequently dig ventilation shafts from their subnivean space up to the snow surface. And as voles visit tunnel openings, owls may sometimes localize them visually. These ventilation shafts certainly guide also the owls' auditory search at times.

It might seem strange that rodents dig tunnels up to the snow surface, which makes them so vulnerable to avian predators. But because of respiration by bacteria, plants, and animals there is often an accumulation of CO₂ in the subnivean space, amounting to up to five times the atmospheric levels; and voles have been shown to avoid regions of high CO₂ concentrations (Penny and Pruitt 1984; p. 377). The tunnels dug by rodents to the snow surface therefore probably serve primarily to reduce CO₂ concentrations in their subnivean home-range.

Some of the northern owls store prey during winter, for instance in tree-holes or on branches near the day-roost. It is done particularly by the pygmy owl, *Glaucidium passerinum*, but occurs also among several others. This behavioural adaptation may be seen as a safeguard against future food shortage in an unpredictable environment, where unfavourable winter weather can drastically reduce prey availability.

Linked to this prey-caching in winter is a "prey thawing" behaviour that has been observed in captive boreal and saw-whet owls, *Aegolius funereus* and *A. acadicus*. When thawing frozen prey the owl assumes a posture on top of the prey similar to that during incubation of eggs; heat is transferred to the prey until it has thawed just enough to be eaten. The thawing of frozen prey involves a substantial energy drain to the owl but the behaviour is essential as it enables the owl to tear apart and eat prey that are stored at freezing temperatures (Bondrup-Nielsen 1977).

The male in *Aegolius funereus* usually makes a deep depression in the bottom material in hollow trees, sometimes a few weeks before the eggs are laid, often even before he has attracted a female. This is

usually the first sign of his nest-site selection (R. Å. Norberg 1964). The reshuffling of the bottom material, and the surface enlargement associated with the depression, speed up thawing, drying up, and warming of the bottom material before egg-laying. Moreover, the female usually stays in the nest for up to a week before laying (R. Å. Norberg 1964), which also may be important for warming the nest in a cold climate.

One additional aspect of evolution among northern owls is that the northward increasing prevalence of cyclic population fluctuations among prey may allow higher evolutionary rates than would otherwise be possible.

During a period of rapid population growth, conditions are obviously favourable. Some aspects of natural selection are therefore relaxed, which should lead to greater variability among the breeding population. This is because genetic variation is in equilibrium between mutation and recombination on the one hand and selection on the other. The survival and reproduction of animals that would not have survived under stricter selection regimes may permit genes to be tested in new genetic combinations. The great opportunities for new genetic recombinations to arise during a period of rapid population increase, followed by the extremely strong selection during the ensuing population decline, should allow more rapid evolution than with a more constant population density (Ford 1964, pp. 11-12). This factor might be important for the origin of ear asymmetry which seems to have occurred at high latitudes in some evolutionary lines among owls.

15. THE GREAT GREY OWL

I will make a few remarks particularly about the great grey owl which figures so prominently in this symposium, and very much so also behind its conception. I start by citing a Swedish naturalist, Erik Rosenberg, who characterized it as follows (my translation from Swedish): "The Great Grey Owl is almost as big as the European Eagle Owl and has a rather fantastic appearance. If the Eagle Owl looks like 'The Horny-headed Devil', then the Great Grey Owl resembles 'Tita Grey' - as may be known, a witch for whom the Devil had the greatest respect" (Rosenberg 1953).

The great grey owl has an enormously thick and fluffy plumage that gives very good thermal insulation against arctic winter temperatures. As a first approximation the great grey owl could be said to consist entirely of feathers! And its grey plumage is probably an adaptation for crypsis among the predominantly grey bark and lichens in the taiga forest. But the grey colour might also increase the thermoregulatory efficiency at low temperatures (see above: "3. Colour morphism").



Figure 23. - Composite picture with a photograph of the skull of a great grey owl superimposed on a photograph of the feathered head, showing the relative sizes of the skull and the facial ruffs and discs. - From Nero (1980, p. 76). Photograph obtained by courtesy of Dr. Robert W. Nero and Robert R. Taylor. Photos: R. R. Taylor.

The great grey owl has rather small eyes with yellow iris, which is unusual for a *Strix* species. The head and face are enormously large for the size of the owl, and the huge facial ruffs and discs are extremely well developed. Indeed, the whole face acts as an external ear, collecting sound over its entire surface area. This suggests the owl can detect very faint sounds made by prey underneath a deep snow cover.

The external ears are asymmetrical and the asymmetry extends also to the skull, the squamoso-occipital wings exhibiting an asymmetry very similar to that in *Strix uralensis*, but not by far as pronounced as in *Aegolius* (figs 8 and 9) (R. Å. Norberg 1977 and 1978).

The great grey owl takes remarkably small prey animals for its size. Indeed, even though it weighs about seven times as much as Tengmalm's owl, *Aegolius funereus*, which is sympatric with it over most of its range, its prey size as well as prey species composition are almost the same (Mikkola 1983, pp. 376, 377; Mueller 1986, p. 391). Not even during periods of extreme food shortage does the great grey owl resort to big prey; irruption owls that were found outside the breeding season in a more or less emaciated condition had not eaten anything but small rodents and shrews (*Microtidae* and *Sorex* spp.; Höglund and Lansgren 1968, pp. 391-394).



Figure 24. - The elusive "Phantom of the Northern Forest" (Nero 1980). - Photo: R. Åke Norberg.

This is in striking contrast with the strong correlations usually observed between raptor mass and prey mass among diurnal birds of prey, for instance among Accipiters (Storer 1966; Opdam 1975; Newton 1979; U. M. Norberg 1981, p. 182). Because of the large size of the great grey owl and its choice of small prey animals, it must take more prey per unit time than smaller owls do. This would seem to put it at a competitive disadvantage with respect to, for instance, *Aegolius funereus*.

Let us therefore look briefly at some compensatory advantages of the large size of the great grey owl. First, its extremely thick plumage should reduce its metabolic energy cost for thermoregulation. Second, its large external ears (essentially the whole face) should collect more sound energy than the ears of smaller owls, particularly for sounds of low frequencies. And since low-frequency sounds carry farther than do sounds of high frequencies (because of increasing diffraction and atmospheric attenuation with rising frequency), the detection distance of prey rustles should be particularly long in the great grey owl. Third, and again because of the large size of the face, interaural time differences are large and the asymmetry of the ears should allow horizontal and vertical localization already at relatively low frequencies, both factors enhancing the accuracy of localization of a sound source.

The mere size of the head and face thus enhances the probability of sound detection and improves localization accuracy. But once a prey that is concealed underneath vegetation, soil, or snow, has been detected, the owl's big size will again prove beneficial. Tryon (1943) saw a great grey owl strike at the ground with considerable force, apparently breaking through the roof of feeding runways in soil,

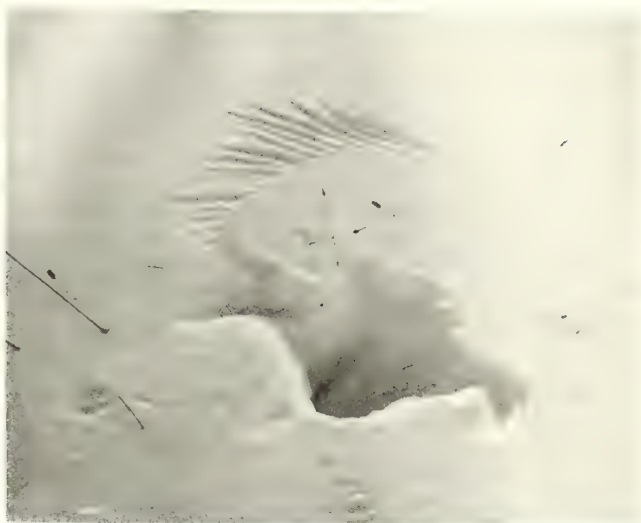


Figure 25. - The big size of the head and face of the great grey owl improves its probabilities of auditory detection of concealed prey and enhances localization accuracy. The asymmetry of the external ears improves sound localization in elevation. Its large weight enables it to make deep plunge-holes in the snow and to catch prey deep below the snow surface where lighter owls could not possibly get at the prey. The photographs show plunge-holes made in snow by the great grey owl. - Photographs obtained by courtesy of Dr. Robert W. Nero and Robert R. Taylor. Photos: R. R. Taylor.



and catching pocket gophers, *Thomomys talpoides*, in their burrows. Goodfrey (1967) reported on a great grey owl catching prey under 20 cm of soft snow. Nero (1980, pp. 89-93) described how great grey owls pounced at prey concealed under snow, and showed photographs taken by Robert R. Taylor (some of which appear in my fig. 25) showing deep plunge-holes, indicating that the great grey owl can get at prey that is moving beneath such deep snow

that lighter owls could not possibly reach it. And, finally, Hildén and Helo (1981, p. 164) showed photographs taken by Eero Kemilä of a striking great grey owl that almost disappeared in the snow, and they also reported an observation by T. Korkolainen who witnessed a great grey owl which plunged through a snow crust hard enough to bear a 80-kg man.

So even though the great grey owl does not use its large size to take big prey, it obviously benefits from its size in other ways.

16. EPILOGUE

Before I stop entirely, I want to add the following. For me to come to this symposium in Winnipeg and talk about the great grey owl and other owls is like "carrying owls to Athens". This is a Greek proverb based on the fact that owls, in particular the Little Owl, *Athene noctua*, were very common around the city of Athens in Greece (Sparks and Soper, 1970, p.161).

But on my way here I met a Greek on the plane, Anastasios Christodoulou. I asked him about this proverb and he gave a different interpretation of it. This relates to the owl being a symbol of wisdom. And since there was so much wisdom in ancient Athens already, there was no need of "carrying owls" there. This very much applies to my situation here at this symposium.

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A Second Chance for Owls (Banquet Address)¹

Katherine McKeever²

The use of permanently damaged wild owls for captive breeding, although difficult to implement, has great merit in providing intimate, continuous observations of how owls use space, avoid stress and form effective pair bonds when multiple choices are available. Surrogate parenting of wild orphans by human imprints is also examined.

The Owl Rehabilitation Research Foundation is situated on the west bank of the Jordan River Estuary, two miles south of Lake Ontario, twenty miles west of Niagara Falls in Ontario Canada. Of the eight acres (3.25 hectares) owned by the Foundation, six acres are on level ground 100 feet (31 metres) above the estuary and two acres slope to the valley floor. This slope supports a remnant Carolinian wood lot of mature Red and White Oak, Hickory, White Pine, Walnut, Dogwood and Tulip Magnolia.

Incorporated as a registered charitable Foundation in 1975, the organization really began a decade earlier as a reception and rehabilitation centre for injured raptorial birds. In the years since, the emphasis first shifted to admission of owls exclusively and then to consideration of the wasted potential in those owls with injuries which precluded release but not restoration of health.

Although the returning ability to function in release is still rewarded with freedom, those owls for which freedom can never be an option are assessed very critically for their potential in a captive breeding program. Obviously, there is little purpose in retaining members of naturally abundant species for further proliferation in such a program, but the Foundation houses several pairs of the most commonly encountered owls as foster parents for incoming orphaned young of these species.

However, permanently damaged members of naturally rare or diminishing species are the prime candidates for a captive breeding program. Much of the available land and income of the Foundation is involved in this endeavour. Currently, there are 54

outdoor compounds, ranging from 200 to 3,500 square feet each (18.58 to 325.15 square metres), the average being 600 to 900 square feet (55.74 to 83.61 square metres). The 41 largest of these are double-territory breeding compounds and 13 are holding and release-training areas. The breeding units presently house 86 permanently damaged residents, representing the 15 Canadian species. To date, 9 of these species have successfully bred on the premises, with infertile eggs following attempted copulation from 3 more (table 1)

Although the fact of these owls having achieved independence in the wild before being injured obviously renders them the most unlikely and difficult prospect for captive breeding (not to mention the

Table 1. -- Owl species native to Canada, all of which are represented at the Owl Rehabilitation Research Foundation.

Common name	Genus and Species	Resident
American Barn Owl*	<i>Tyto alba</i>	2
Screech Owl *	<i>Otus asio</i>	9
Flammulated Owl ⁺	<i>Otus flammeolus</i>	5
Great Horned Owl*	<i>Bubo virginianus</i>	6
Snowy Owl*	<i>Nyctea scandiaca</i>	7
Northern Hawk Owl ⁺	<i>Surnia ulula</i>	6
Northern Pygmy Owl*	<i>Glaucidium gnoma</i>	7
Spotted Owl ⁺	<i>Strix occidentalis</i>	2
Barred Owl ⁺	<i>Strix varia</i>	6
Great Grey Owl*	<i>Strix nebulosa</i>	7
Long Eared Owl	<i>Asio otus</i>	2
Short Eared Owl	<i>Asio flammeus</i>	5
Boreal Owl*	<i>Aegolius funereus</i>	6
Saw-whet Owl*	<i>Aegolius acadicus</i>	8
Burrowing Owl*	<i>Athene cunicularia</i>	8

*Species which have produced offspring.

⁺Species which have produced eggs only.

¹ Paper presented at the symposium, Biology & Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

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physical limitations imposed by their injuries) success is both justifying and intensely interesting. The very fact of their intransigent wildness makes them valuable beyond any comparison with domestic stock.

Selecting that part of the acreage which most closely resembles the habitat of the species (Fig.1) the challenge to this Foundation has been to design and erect breeding compounds of such size and diversity that they offer every imaginable choice to the wild occupant. (Fig.2)

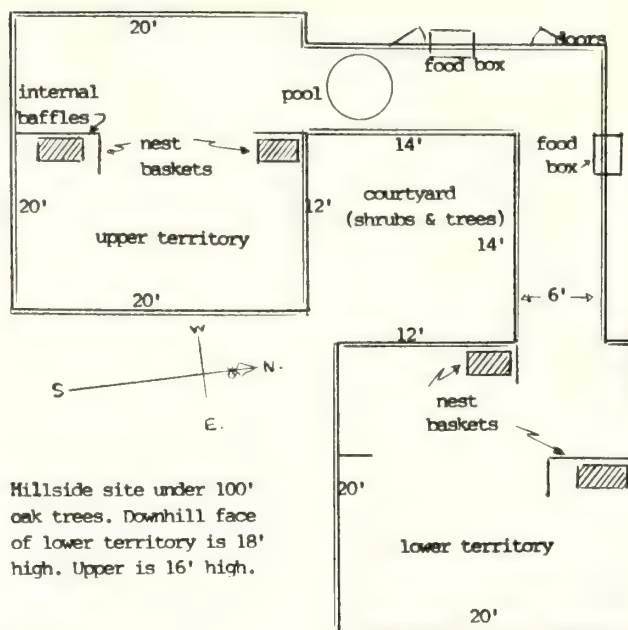
Just as the provision of choice is the most critical ingredient in any enclosure for wild owls, it is also the most important aspect of their relationship with a potential mate. Thus, having provided continuous perimeter flight paths as 'escape routes' for the male, it is encouraging to see that his approach to the female is made confident by his awareness of that escape route, whether or not he is ever obliged to use it. The whole process of being able to choose, whether it be a territory, a nest site, a favoured perch, a private food source or just being able to get away from each other, is the route to psychological security for the permanently damaged wild owl and the ONLY route that will lead, ultimately, to spontaneous breeding.

Human interference at the Foundation is pared to the absolute minimum possible. Nesting areas are never entered during the season, except in a medical emergency. Pools are serviced and prey provided in hunting areas only. Eye contact is avoided and observations are made from screened areas. The Foundation is never open to the public and visitation is by appointment only.

All progeny hatched on these premises are raised entirely by their natural parents, away from the sight of, or interference by, humans and are as wild as their parents. They are handled only twice,



Figure 1.--One corner of 800 sq.ft.(74.32 metres) breeding compound for one pair of Spotted Owls (*Strix occidentalis*). Downhill face is 17' high (5.23 metres).



Hillside site under 100' oak trees. Downhill face of lower territory is 18' high. Upper is 16' high.

Figure 2.--Design of 1,004 sq.ft. (92.9 metres) compound in which one pair of damaged Great Grey Owls (*Strix nebulosa*) have bred.

once when they are removed to release-training compounds, and for the last time when they are banded and shipped for release to the area where one of their parents originated. The release-training itself involves four weeks of learning to forage for unseen live prey under suitable cover and for the more nocturnal species especially it accomplishes the transition from visually perceived prey to that located by sound reception. Owls which fail to demonstrate this ability, whether hatched here, received as orphans or following rehabilitation are not released.

Beyond the utilization of physically damaged wild owls in a breeding program, there is also a very positive function provided by owls which are damaged in a different way - by disorder of their relationship formation with their own species and orientation towards human life forms instead. The Foundation has received a number of such human imprints over the years and three of them are among the most useful owls we have ever admitted. Two of these, a male Great Horned Owl and a male Screech Owl are themselves members of locally common owl species and each year provide both sustenance and imprint re-inforcing for incoming fledgelings of their species.

Since the human imprinted adults are easily manipulated by their human 'mates', they serve in an intermediate capacity between the human on one hand and the wild but still vulnerable juvenile on the other, and make it possible for the human to control the nutrition of the young owl without the danger of being visible to it during the imprinting period. Species imprinting is safely established

when the young owl clearly recognizes the DIFFERENCE between the image of the 'safe' parent and that of other animate life forms. This milestone is marked by instinctive defense posturing and beak snapping when the owlet is confronted by an alien image. Thus safely oriented towards their own species, the young are then processed through the facility along with those hatched on the premises.

The third human imprint owl in service at the Foundation is in many ways the most useful of all, by virtue of being a female of a medium-sized species (Spectacled Owl; *Pulsatrix perspicillata*). Encouraged by her human 'mate', with grooming and hand feeding, to produce an egg at the beginning of the ambient nesting season for native owls, she will then accept any other egg of even faintly similar size and incubate it faithfully to hatch. Although a model incubator, superior to any mechanical device, she truly excels at motherhood! It is the author's contention that the psychological security developed in the nestling infant by the solicitous brooding mother is just as critical to future performance of the owl as it is to that of primates and humans. (Fig.3)

The only limitation in using this remarkable owl as a surrogate parent is that before visual focus is achieved the nestling must be transferred to the care of an adult of its own species. Indeed, the Spectacled Owl is often by-passed as a foster parent when breeding residents of the orphan's own species are brooding young of comparable size. The Spectacled Owl can be seen as insurance against the day when incompatible eggs or orphans are presented. Nevertheless, in one memorable year, this owl 'processed' five nestlings of four species over a four and a half month period, in each case



Figure 3.--Human imprint Spectacled Owl (*Pulsatrix perspicillata*) brooding Barn Owl (*Tyto alba*) chick which she has incubated to hatch.

reverting to appropriate feeding for a newly hatched infant and raising it through degrees to the point of swallowing whole prey!

In reviewing the justification for a captive establishment for permanently damaged WILD owls, the author recognizes that the best that can be achieved will never be as effective as leaving the owl alone, undamaged, in his own environment. Obviously, this will always be second best, really only salvage and tenuous at that. But it is better than doing nothing about the carnage, and it does offer intimate and continuous observations of the kind not easily supported in the field. Patterns of behaviour in individual owls are so strong that one can predict where the owl will be and what he will be doing at almost any time of day or evening. Anomalies in these patterns can then be studied for their origin and manifestation and especially for their indications of change. Our residents live long lives and go about their daily activities, crippled but not defeated, constantly trying and sometimes succeeding in passing on their genes so that their progeny can be released in their place. (Fig.4)

It is always deeply satisfying to return to the wild population some part of the genetic diversity diminished by the injury to the parent. It is even more rewarding to see the capacity for survival and function in a truly wild raptor when dignity is regained through the ability to make choices. Returning self confidence allows the damaged raptor to resume his inherent behavioral patterns of territorial defence and mate solicitation, even though, of necessity, under the umbrella of protective captivity.



Figure 4.--Partially fledged siblings from breeding pair of permanently damaged wild Saw-whet Owls (*Aegolius acadicus*).

Distributional Status and Literature of Northern Forest Owls¹

Richard J. Clark,² Dwight G. Smith,³ and Leon Kelso⁴

Abstract.--The literature for the 22 species of owls designated as "Northern Forest Owls" [for purposes of this symposium] was examined via analysis of 6,590 articles cited in Clark, Smith and Kelso (1978) plus an additional, estimated 3500 references. Articles were categorized according to geographic location, chronology, informational content and species. While some general trends were identified no single factor could satisfactorily explain the presence or absence of quantities of articles dealing with each species. Based on the summary of the literature and this symposium five (5) owl species are identified as "**species of special concern**" for researchers, wildlife specialists and land managers.

INTRODUCTION

This report deals with all 22 of the species designated by the conference committee for this conference as northern forest owls, i.e., those species associated with the forest and with the 35th parallel designated as their southern border. Any species occurring wholly below this line has not been considered a "northern forest owl." The scientific literature on the 22 species of northern forest owls is published in the journals, bulletins and other formats of a number of publications throughout the world with those of Eurasia and North American countries predominating because of the ranges of the species and human population centers. Some literature, especially the early literature published prior to the advent of abstracting services, is not readily available and therefore usually not as well known. In addition, the literature on owls published in eastern European countries is generally not easily accessed by North American

Strigiologists and probably the reverse is also true.

Our bibliography of owl literature (Clark *et al.* 1978) included 6590 references on the published literature of all the world's owl species known at that time. To this we have added approximately 3500 additional references, many of them published since 1978. Using this reference data base, we herein (1) summarize the extent and distribution of the available literature on northern forest owl species; (2) describe the temporal and geographic origin of this literature; and (3) provide brief summaries of the literature trends per species. Based on this analysis, we describe the major categories of literature published on each species and provide an inventory of logical areas of research not yet investigated. We also describe the distributional status and range of each species.

METHODS

Information on the range and distributional status of each of the northern forest owls was determined from the literature. For some species the range was plotted from several published sources. The geographical area occupied by each species was determined by tracing the range on standard survey maps, cutting the plotted range, weighing the cutout on a Mettler PC2000 digital balance and comparing the weight with a

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known area/weight ratio. Results provided a basis for the comparison of the areal coverage of each northern forest owl species range. This method does not, of course, take into consideration the fact that not all areas within the boundaries delimited on such a map will possess suitable habitat for that particular species. The results are thus only rough approximations of extent of geographic distribution. Information on the literature of each owl species was determined using methods described in Clark *et al.* (1978). Briefly, we extracted the references using computer search services [such as the suitable data bases within Lockheed's DIALOG], checking abstracting publications including Zoological Record and Biological Abstracts and searching journals issue by issue. Most of the estimated 3500 new references were obtained from this source with many having been obtained by authors or researchers having sent the senior author listings of references not listed in Clark *et al.* (1978). Data obtained for each reference included authorship, date of publication, journal or other publication format, topics covered and geographic locale of the observation or investigation.

Topic coverage [which we have termed "ASPECT"] of each article was assigned as one or more of eight broad categories: "ecology", "behavior", "distribution", "taxonomy", "physiology", "anatomy", "conservation" and "general". Many articles included information which was assigned to several categories. The "general" category was limited to articles which were primarily intended for a nonscientific audience.

Each article was also assigned an appropriate code indicating the GEOGRAPHIC LOCATION for the report. There were 112 listings with Australia, Canada and the United States being broken down into states or provinces. This was done because the literature from those areas tended to be more recent and the political boundaries somewhat more stable.

In addition each article was also assigned an appropriate code indicating the Genera or Genus for the report. There is a considerable problem with this because of difficulties associated with the dynamics of nomenclature and changes in taxonomy resulting from new knowledge of the taxonomic relationships of owl species. One example should suffice to reveal the nature of these problems, e.g., our table entitled "Common names of owls in selected foreign languages," lists 39 common names for *Otus* *scops* and 41 common names for *Strix* *aluco*.

RESULTS

Distribution and Status

General works which describe the distribution and ecology of owls, including the northern forest owls is presented in Burton (1973) and Grossman and Hamlet (1966). The owls of Europe are described in greater detail by Mikkola (1983) and of Asia by Dement'ev *et al.* (1966).

A summary of the distribution, ecological habitat and status of the 22 species of northern forest owls is presented in Table 1. The Long-eared Owl, Hawk Owl, Great Gray Owl and Boreal Owl are holarctic occurring in both new and old world hemispheres. Of these, the Long-eared Owl is the most wide-ranging and encompasses the largest geographical area of any species of northern forest owl. The Great Gray Owl, Boreal Owl and Hawk Owl may more correctly be classed as circumboreal since they occupy coniferous forest habitat and its successional stages, except during their southward incursions. Although more restricted in distribution, the Eagle Owl, Great Horned Owl and Scops Owl also have a wide areal range coverage. All three may be considered habitat generalists. The Eagle Owl occurs in a wide variety of habitats in Europe, Asia and Africa while its new world kin, the Great Horned Owl, occupies deciduous, coniferous, mixed and riparian woodlands, desert scrub, and other habitats in North, Central and South America. The Saw-whet Owl is something of an exception to the rule that an owl must be a generalist to have a large areal range coverage. Being a wide-ranging species in North America, it occurs mostly in conifer or mixed woodland. This species has a comparatively small home range and can apparently take advantage of small stands of conifers that occur as natural successional stages throughout much of North America. Conversely, several species have comparatively small ranges, including the Spotted Owl, Flammulated Owl and Western Screech Owl, all occurring in western North America. Of these, the Spotted Owl apparently requires large tracts of relatively undisturbed woodland or forest while the Flammulated Owl occurs mainly in montane deciduous woodland.

Literature Synopsis

The literature on northern forest owls includes a minimum of 3800 references which comprises approximately 38% of our accumulated references on owls. These represent studies and reports from virtually every Eurasian and North American country. Geographically, approximately 52% of these references are from North American sources and 48% from Eurasian, principally European sources.

Table 1.--Distribution, status and habitat of Northern Forest Owls.

SPECIES	DISTRIBUTION	AREA(km ²)	HABITAT / STATUS
Flammulated Owl (<i>Otus flammeolus</i>)	North America: sw Canada, w US, s to Guatemala.	2,043,267	Montane conifer forests.
Eastern Screech-Owl (<i>Otus asio</i>)	E N. America: s Canada to Fla. and Gulf Coast, w to c Texas and the front range of the Rocky Mts.	5,408,650	Deciduous woodland, riparian wood, orchards, urban open space / most common bird of prey in sub-urban and urban open space.
Western Screech-Owl (<i>Otus kennicotti</i>)	W N. America: sc Alaska to highlands of c Mexico, e to Rocky Mts., Rio Grande.	3,846,150	Riparian and Oak woodland, cactus desert / earlier treated as Eastern Screech-Owl subspecies; NOT REPORTED ON AT THIS SYMPOSIUM!
Common Scops-Owl (<i>Otus scops</i>)	C and s Eurasia, Asia Minor, nw Africa, s of Sahara except Congo basin.	21,394,209	Widespread, deciduous and coniferous woodland, riverine wood, thornbush, parks, gardens, savanna: NOT REPORTED ON AT THIS SYMPOSIUM!
Striated Scops-Owl (<i>Otus brucei</i>)	C and se coastal Arabian peninsula.	3,822,112	Sometimes grouped as a subspecies of Common Scops-Owl; NOT REPORTED ON AT THIS SYMPOSIUM!
Oriental Scops-Owl (<i>Otus sunia</i>)	S Asia, India, se Asia, n to ne Russia, China, Korea and Japan.	12,019,219	Sometimes grouped as a subspecies of Common Scops-Owl; NOT REPORTED ON AT THIS SYMPOSIUM!
Collared Scops-Owl (<i>Otus bakkamoena</i>)	E Asia, from India, se Asia China, n into Korea and along coast, Indonesia, Philippines, Japan.	13,103,317	Woodland, savanna, parks and gardens: apparently common especially in cultivated areas; NOT REPORTED ON AT THIS SYMPOSIUM!
European Eagle Owl (<i>Bubo bubo</i>)	Eurasia, including India, China, n to tundra, Iberian Peninsula and n Africa, into Asia Minor.	47,475,915	Widespread, temperate and tropical forests, cliffs, outcrops in the desert, cultivated areas / Suffers from local extirpation, reintroduction programs are counteracting some of this.
Great Horned Owl (<i>Bubo virginianus</i>)	North America s of tundra, Central America and South America to Straits of Magellan.	33,533,620	Widespread, forests, deserts, mountain forests, rain forests to limits of woodland, mangrove / Similar to European Eagle Owl it is sometimes persecuted by man because of its "competition".
Blakiston's Fish Owl (<i>Ketupa blakistoni</i>)	Northeast China, Korea, e Siberia.	4,447,030	Coastal areas, riparian woods / Rare and little known species; NOT REPORTED ON AT THIS SYMPOSIUM!
Northern Hawk-Owl (<i>Surnia ulula</i>)	Holarctic: North America from n US into Alaska, Canada, Eurasia, Scandinavia, n Russia.	36,177,848	Clearings and patchy areas of northern conifer forest, low scrubs and trees near water.
Northern Pygmy-Owl (<i>Glaucidium gnoma</i>)	Nw North America, w Canada, w US, s into Mexico and Central America.	4,470,913	Montane Pine-Oak wood, mature conifer and mixed woodland.
Eurasian Pygmy-Owl (<i>Glaucidium passerinum</i>)	Central Europe e to extreme e coast of Russia, southern Scandinavia and Finland.	9,191,846	Conifer and mixed woodland.
Oriental Hawk Owl (<i>Ninox scutulata</i>)	Asia: India, China, se Asia, Japan, Indonesia, Philippines.	13,210,808	Widespread in forests and cultivated areas, mangroves; NOT REPORTED ON AT THIS SYMPOSIUM!
Barred Owl (<i>Strix varia</i>)	North America, s Canada, e US, s to Gulf Coast, s into Mexico and Central America.	7,922,466	Dense deciduous or coniferous woods, near lakes, streams, swamps / has been extending its range w in North America.

Table 1. (continued)--Distribution, status and habitat of Northern Forest Owls.

SPECIES	DISTRIBUTION	AREA(km ²)	HABITAT / STATUS
Spotted Owl (<i>Strix occidentalis</i>)	North America, sw Canada, w US, s into highlands of Mexico.	2,740,938	Dense conifer forest and wooded ravines and canyons / Endangered list because of widespread forest destruction within its range.
Great Gray Owl (<i>Strix nebulosa</i>)	Circumboreal: North America, n US, Canada s of tundra.	29,927,855	Northern coniferous forest.
Tawny Owl (<i>Strix aluco</i>)	Palaearctic: Europe into Asia Minor and c Russia, Himalayas se Asia, Korea and Japan.	20,793,248	Deciduous woodland, cultivated areas, urban open space / Hume's Owl considered by some to be a subspecies of the Tawny Owl is endangered.
Ural Owl (<i>Strix uralensis</i>)	Eurasia: s Scandinavia, ne Europe, c Russia, Siberia, Korea and Japan.	20,802,457	Mixed and coniferous forest.
Long-eared Owl (<i>Asio otus</i>)	Holarctic: North America from n US to n Canada; Europe and c Asia, e to Japan. Nw Africa.	48,066,990	Coniferous and mixed deciduous forest, cultivated areas with trees.
Boreal or Tengmalm's Owl (<i>Aegolius funereus</i>)	Circumboreal in coniferous forests of North America and Eurasia; n to Tundra, s to deciduous forest-prairie ecotone.	38,822,077	Circumboreal coniferous forest also mixed forest of pine, birch and poplar.
Northern Saw-whet Owl (<i>Aegolius acadicus</i>)	North America: southern Canada, US s into Mexican highlands.	10,516,816	Dense woodland, cedar and tamarack swamps.

Note: All of the tabled species were designated appropriate subject species for this symposium. Nearly all of those species bearing the status comment "NOT REPORTED ON AT THIS SYMPOSIUM!" (with the possible exception of the Common Scops-Owl) should be considered SPECIES OF SPECIAL CONCERN for researchers.

This, however, may illustrate the difficulty of obtaining European references rather than a slight imbalance in work on Strigiformes. In North America the majority of literature is from the United States with lesser amounts from Canada, Mexico and Central American countries. In Europe, most published owl work originates from Germany and England, although collectively the Scandinavian countries have contributed a number of very important reports of investigations.

Looking at the various aspects reported in the literature for all species [Figure 1] we can see some general trends, e.g., ecology, distribution and behavior were the predominant aspects reported on for nearly all species. In examining the pie graphs for the individual species, those three categories generally make up at least 75% of the literature aspects. This is, perhaps, a result of the way in which the aspects were defined, e.g., ecology tends to be an encompassing term and while we tried to use that designation only when ecology was emphasized, studies involving a species

interaction with another species, or the environment of the species also had to be categorized as "ecological." The designation "distribution" was used when specific geographic locale(s) for a species was/were given and our rule of thumb in using this designation was--was enough information given that the article "plotted a point or points" where the species was found? Behavioral information is provided whenever living individual(s) of the species were discussed. The remaining categories of aspect, thus, remain areas where more research is needed, i.e., conservation, taxonomy, physiology and anatomy.

In terms of the absolute number of references, the Great Horned Owl and Eagle Owl have been the topic of the greatest number of papers, followed by the Long-eared Owl. Conversely, several species such as Blakiston's Fish Owl, Collared Scops Owl, Oriental Scops Owl and Oriental Hawk Owl have been investigated less, and are known mostly from anecdotal and range accounts published in field guides and publications exemplified by Dement'ev's

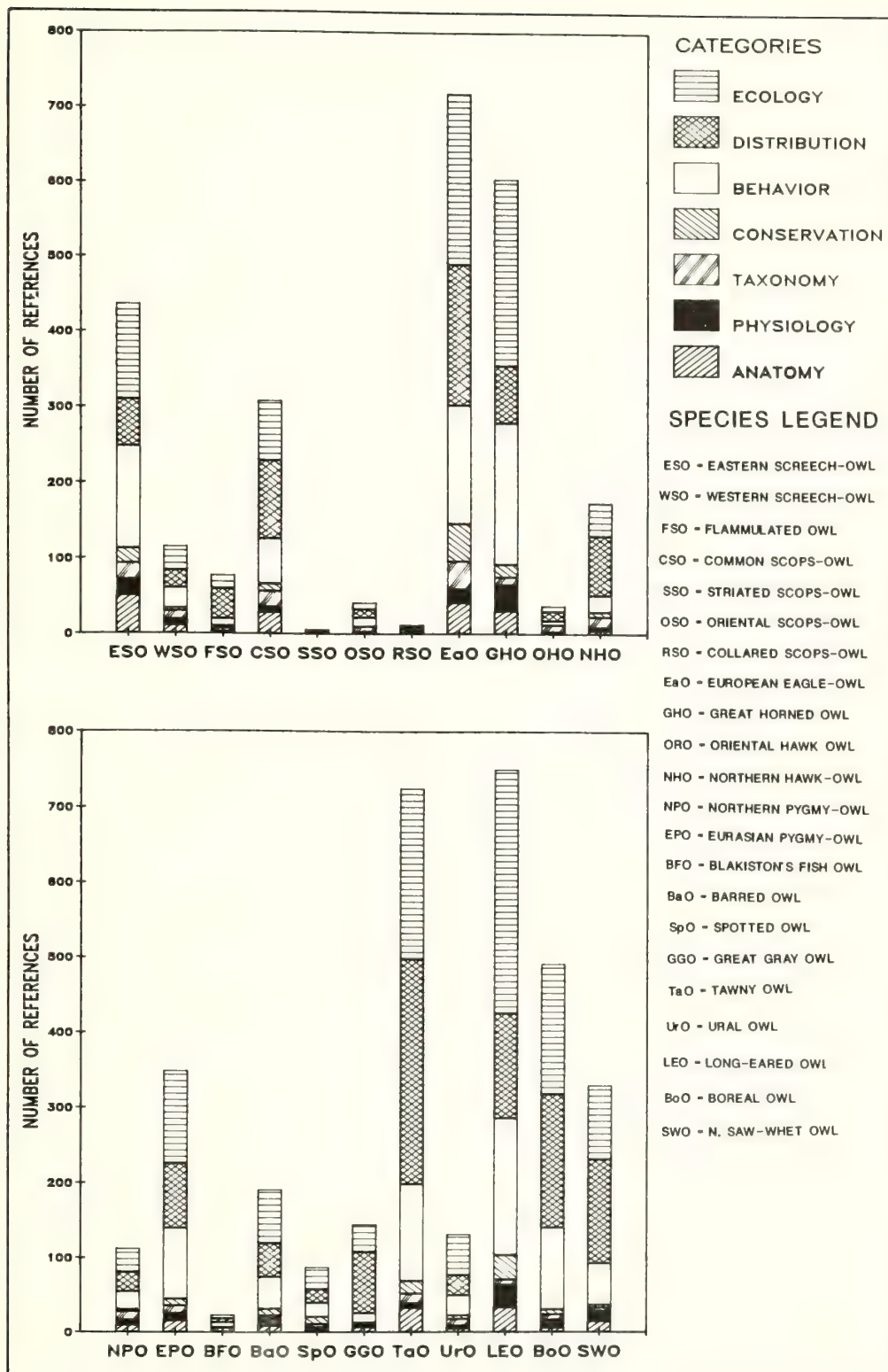


Figure 1.--Summary of literature on owls of the "Northern Forest" by species and informational category. Species legend covers all 22 species designated for this symposium. Articles were identified from the 6,590 cited in Clark, Smith and Kelso (1978). In nearly all species the information content of articles is at least 75 - 80% ecology, distribution and behavior.

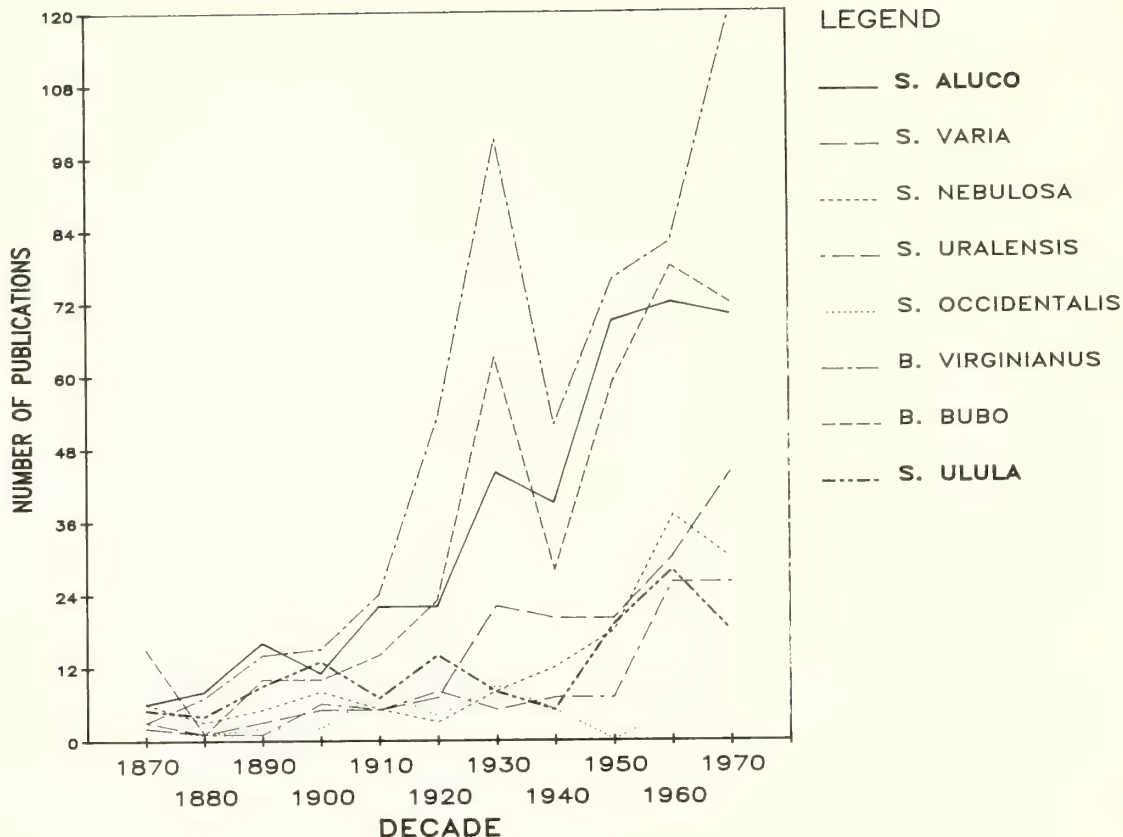


Figure 2.--A century of literature on eight owl species reveals 1) a general upward trend for nearly all species with a "burst" of articles in the 1930's, a decline in the WWII years and then a resurgence beginning in the 1950's and 2) a dichotomy with a few species being relatively well studied and a larger number only recently becoming subject for considerable study.

"Birds of the Soviet Union" and similar works.

Chronology

While the references date from 1842 most of the literature has come within the last 50 years, i.e., from 1930 to the present. We did not plot the chronology for all species (see Fig. 2) due to the lack of space but rather selected a cross-section of species. The same general trend was observed in all species. Much of the early literature is imbedded within general works, e.g., faunal treatments, thus making it difficult to locate and to cite.

Genera and Species Discussion

Strix Species

Northern forest owls include five species of *Strix* for which we have located a total of 873 publications (see Fig 3). Of these, 46.8% concern the Tawny Owl (*Strix aluco*), 17.4% the Great Gray Owl (*Strix*

nebulosa), 16.8% the Barred Owl (*Strix varia*) and 7.1% the Spotted Owl (*Strix occidentalis*).

Excepting the Tawny Owl, the most common category of topic coverage is ecology, which averages about 32% for each of the *Strix* species and 30% for the Tawny Owl literature. Distribution is the most common topic of papers on both the Great Gray Owl (50.7% of topics) and the Tawny Owl (39.7% of topics), followed by ecology.

For all five species the least frequent topics were physiology, anatomy, conservation and taxonomy. About 10% of papers on the Spotted Owl were concerned with aspects of its conservation, reflecting in main the limited knowledge of the status of this *Strix* species and loss of its forest habitat in the western United States.

The Great Gray Owl is the only circumboreal *Strix* species. The North American literature on this species originates from 18 states and five Canadian provinces, and in Eurasia from eight countries. Most of the literature on this species is from North

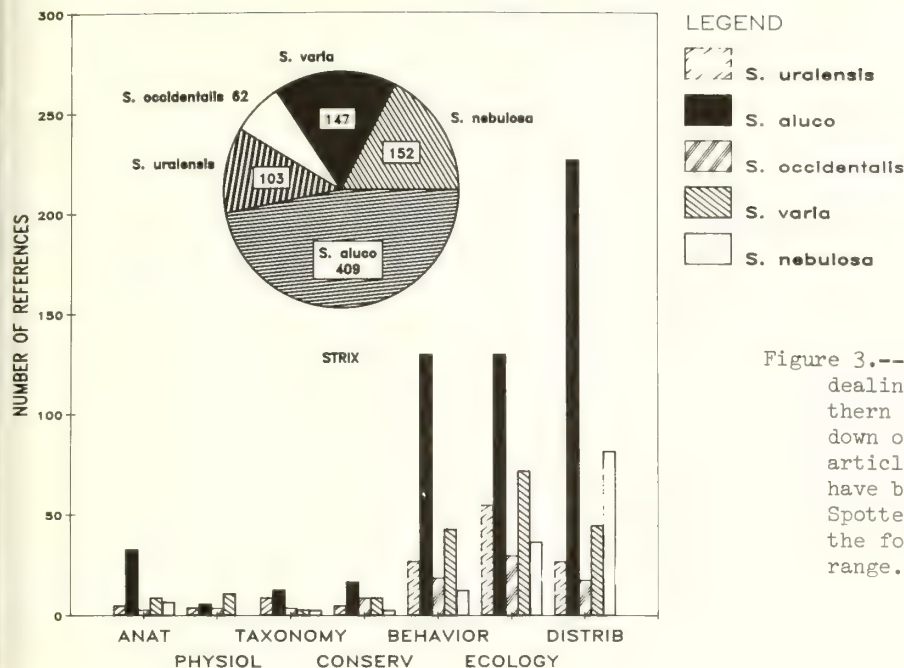


Figure 3.--Summary of the total number of articles dealing with the five *Strix* species of northern forest owls (pie chart) and a breakdown of the informational content of those articles (legend). Although more articles have been written about the Ural Owl than the Spotted Owl, this fact is misleading in that the former has a much greater distributional range.

America (72.4% of published papers) and of this, 42.6% originates from the United States, mostly from Minnesota and Massachusetts. Three European countries, Finland, Sweden and Germany have contributed

the bulk of the European literature. Literature of the Tawny Owl originates from 15 European and three Asian countries. Of these, the great majority are from Germany, which has the astounding total of 142 (34.7%) of Tawny Owl papers, and England, 121 (29.6%). Ural Owl papers originate from 12 European countries and two Asian countries. Most are from Germany (19.4%), Finland (17.3%) and Sweden (15.4%) in Europe while 6.8% are from Japan in Asia. Barred Owl literature is from four Canadian provinces, 28 states and the District of Columbia, while the literature on the Spotted Owl has a much more restricted distribution, originating only from four western states, with 33.9% from California and 19.4% from Oregon.

Aegolius, Asio and Bubo species

We have selected summary diagrams for five species of the above three Genera, after much deliberation over which of the many diagrams were most instructive, based on the following criterion: 1) the Aegolius species were selected because they are small and one [acadicus] is found only in the New World while the other is found in both the Old and New World, thus giving some information that might serve as a basis for comparison of the amount of research that

has been done between the Hemispheres, [see Fig. 4]; 2) Asio was selected as a medium-sized owl that is widely distributed throughout the world, thus giving us some clues as to where in the world it has been most studied and where further work is generally needed [see Fig. 5]; and 3) Bubo was selected because there are two large species, one confined to the Old World and the other the New World so that comparisons similar to the above might be made [see Fig. 6].

CONCLUSIONS

The owls of the northern forest, 22 species in number, make up about 16% of the known species of owls of the world. The literature that we have identified as dealing with these species includes about 3800 articles or about 43% of the literature that we know of. There is, of course, more as yet unidentified. We do feel, however, that we can draw some conclusions from this large sampling, e.g., seven species out of the 22 designated for this symposium were not reported on here. Of those seven species, the literature for five species totals only 72 articles or about 0.7% of all of the literature. Those five species; the Striated Scops-Owl (Otus brucei) [5], the Oriental Scops-Owl (Otus sunia) [29], the Collared Scops-Owl (Otus bakkamoena) [9], Blakiston's Fish Owl (Ketupa blakistoni) [11] and the Oriental Hawk Owl (Ninox scutulata) [18] thus show up as species for which there is a severe shortage of information!

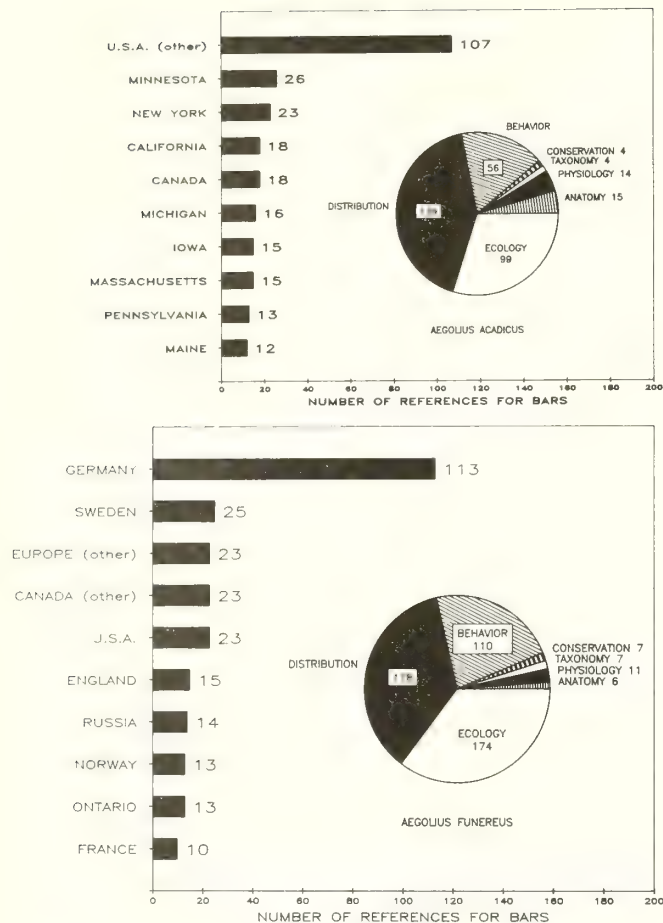


Figure 4.--Comparison of informational content, extent of study, and geographic distribution of the literature on Northern Saw-Whet (upper) and Boreal or Tengmalm's Owl. The former is confined to North America, while the latter is also found in northern Europe also. Note the same three informational categories predominate.

When the National Wildlife Federation was preparing the final copy for our bibliography we asked them to use the Spotted Owl (*Strix occidentalis*) as a model for the artwork for the cover. We did this because we saw that as a species badly in need of research. Since publication of the bibliography in 1978 there has been considerable research done on that species and some of that need for research has been met. We are sure that much of the interest for that species has arisen from its

Figure 6.--Comparison of the large Great Horned Owl (upper) and its ecological counterpart the Eurasian Eagle Owl (lower) shows the same three informational categories prevail as for the other species compared.

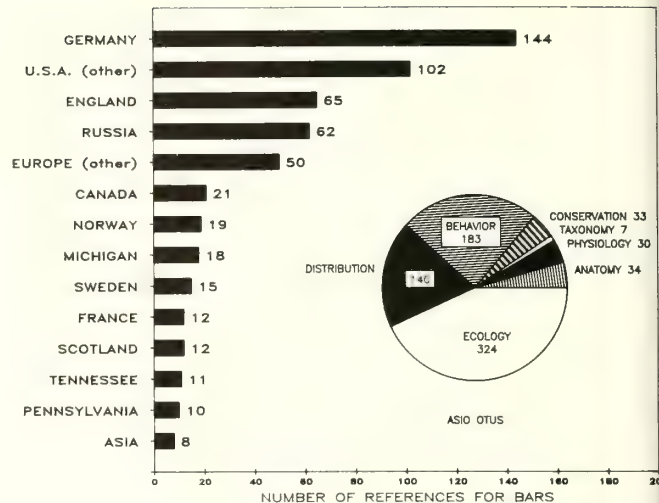
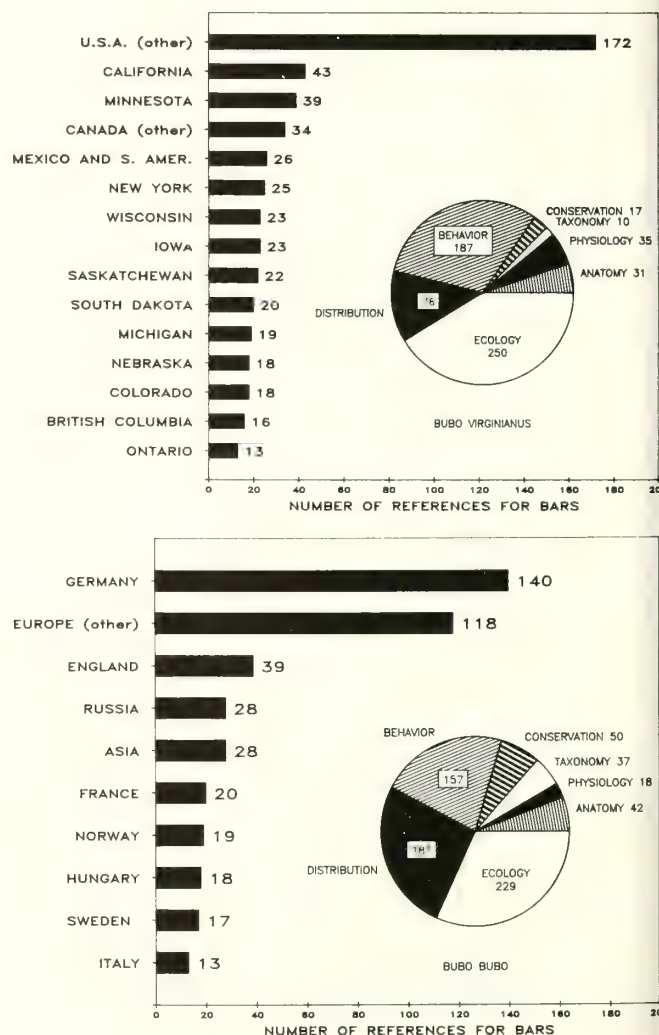


Figure 5.--The trend in the literature of the most widely distributed northern forest owl, the medium-sized Long-eared Owl, is quite similar to that of the smaller owls.



designation as an Endangered Species. We are here designating the above five species, i.e., the Striated Scops-Owl, the Oriental Scops-Owl, the Collared Scops-Owl, Blakiston's Fish Owl and the Oriental Hawk Owl as SPECIES OF SPECIAL CONCERN for researchers in order to call attention to the urgent need for information on those species. The urgency arises from the alarming rate at which habitats for wildlife are being destroyed. While we have identified the need for information for certain species we have also identified a need for communication with regard to information that currently exists in the literature. Much of the literature is not readily available to the conservationists and wildlife and land managers who have a need for the available literature. There are computerized databases available that can get a person with the need to know into some of the literature but they do not approach completeness in their coverage and fairly extensive search strategies are sometimes required to access the literature. Bibliographies are extremely difficult to obtain funding for as most of the conventional sources of funding are not available for such publications. They are reference works with perhaps a select "clientele," but they are critically needed. Governmental agencies or wildlife conservation organizations would do the owls [as well as other wildlife forms] a great

service if they would actively seek working bibliographies and support their preparation and publication. Authors, utilizing bibliographies, can also further the cause by citing bibliographies in their research publications.

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Nearly Synchronous Cycles of the Great Horned Owl and Snowshoe Hare in Saskatchewan¹

C. Stuart Houston²

Abstract.--In the aspen parkland of Saskatchewan, Great Horned Owl reproductive success is cyclical and appears to follow closely the numbers of the Snowshoe Hare, its main prey item. In peak years, nearly all owls nest, some raise four young, and they fledge an average of 2.5 young per successful nest.

INTRODUCTION

A 30-year study of Great Horned Owl productivity included banding of 4285 nestlings in 1883 successful nests. Changes in numbers and reproductive success were roughly coincident with the 10-year cycle of the Snowshoe Hare, (*Lepus americanus*), though as with the lynx, the owl may sometimes peak a year after the hare.

The 10-year cycle of the Snowshoe Hare has been documented for over 100 years. The famous explorer, mapmaker and fur trader, Peter Fidler, gave the following report from Dauphin House, Manitoba, in 1820: "There are in some seasons plenty of rabbits, this year in particular, some years very few, and what is rather remarkable, the rabbits are the most numerous when the cats [lynx] appear. . . . the cats are only plentiful at certain periods of about every 8 or 10 years, and seldom remain in these southern parts in any number for more than two or three years."

Similarly, Dr. John Richardson, surgeon and naturalist with the first and second Franklin expeditions in the 1820s, wrote: "the Canada lynx is the animal which perhaps most exclusively feeds upon it [the hare]. It has been remarked that lynxes are numerous only where there are plenty of hares in the neighbourhood. At some periods a sort of epidemic has destroyed vast numbers of hares in particular districts, and they have not recruited again until after the lapse of several years, during which the lynxes are likewise scarce."

Lloyd B. Keith's well-researched book, *Wildlife's Ten-year Cycle*, includes many graphs from Hudson's Bay Company pelt collections and other sources. These demonstrate the approximate 10-year cycle of the hare and lynx as well as the one or two year lag in peaks and troughs between different geographic regions. The Ruffed Grouse cycle was almost synchronous with the hare's, but at that time data were inadequate for the Great Horned Owl. Later, long-term studies by Keith and associates in the mixed forest at Rochester, Alberta, provided evidence that Great Horned Owl numbers and reproductive success were quite clearly synchronous with Snowshoe Hare numbers (Rusch et al 1972).

METHODS

A relatively small number of observant, helpful farmers and rural schoolteachers have provided fairly consistent effort in finding nests each year. However, I exhorted them to extra searching in the low-hare years of 1984 and 1985, since nest sample numbers had been very low during the previous bottoms of the cycle in the 1960s and 1970s. With extremely few exceptions, every active nest reported within a wide study area was visited and the young banded.

Skewing of Nest Numbers

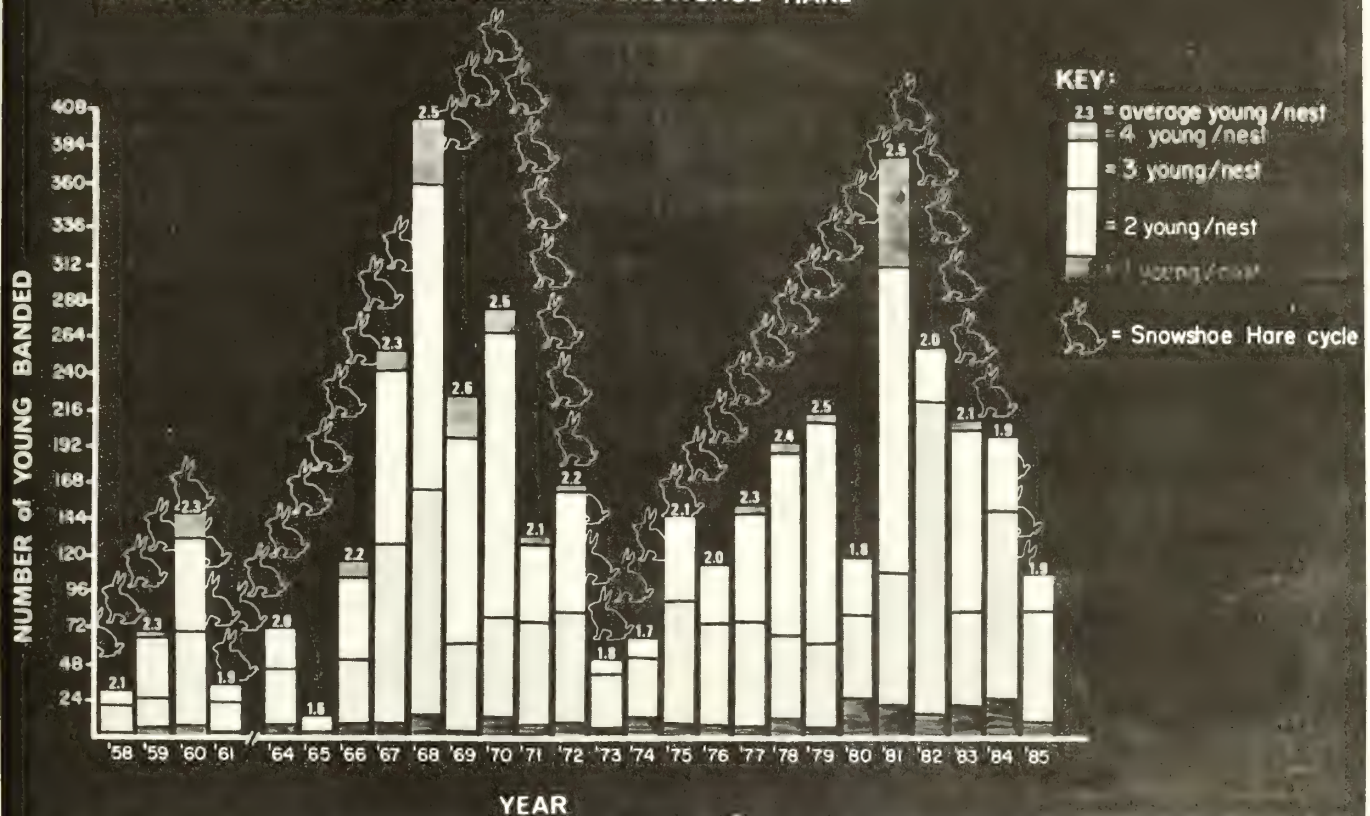
The nest total was skewed upwards in two years. In 1967, two assistant tree climbers, Doug Whitfield and Jon Gerrard, made a special effort and found over 30 nests themselves. In 1968, Whitfield found ten nests and this one year we also went further southeast to 21 nests near Indian Head and Lemberg, an area later covered by Lorne Scott of Indian Head. Total young banded in these two years was thus disproportionately high. Nest success was skewed downwards in 1982 when a forest tent caterpillar invasion almost filled the aspen forest with thick webs, apparently impeding hunting by the parent owls.

¹Paper presented at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

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RESULTS

10-YEAR CYCLE of GHO vs. PEAKS in SNOWSHOE HARE



Comparable Hare, Lynx and Goshawk numbers

Hares were monitored numerically at Rochester, Alberta, from 1964 through 1976, but similar numbers are not to my knowledge available for any Saskatchewan locality. The numbers of lynx trapped each year between 1920 and 1984, an indirect indication of hare numbers, have been published for Alberta and show peaks varying from 8 to 11 years apart, averaging 9.6 years (Todd 1985). Owls peaked in Saskatchewan in 1981. The lynx "crash" occurred in Alberta in early 1982. Goshawks, responding to the hare crash, left the forest and appeared in peak numbers in Duluth, Minnesota in 1972 and 1982 (R.F. Green, pers. comm.)

RESULTS

At the peak of the 10-year cycle of the Snowshoe Hare, nearly 100% of Great Horned Owls breed, with up to one pair for each 5 km² of aspen parkland habitat. They produce an average of 2.5 young per successful nest; only in the years at the top of the cycle are nests with three young in the majority, while some pairs fledge four young (fig. 1). At such times, Snowshoe Hares are extremely numerous. Some owls use nest

sites in more conspicuous locations near roads, that weren't utilized in the years when demand was less. Nests are easier to find.

When Snowshoe Hare numbers crash, most Great Horned Owls move away, some into grassland habitat where production is sustained at a lower level by the less cyclic White-tailed Jack Rabbit (*Lepus townsendii*). Others travel southeast to winter as far away as Nebraska and Iowa (Houston 1978; Houston mss.). For those owls remaining there is insufficient food in late winter. Less than half of the remaining owls attempt to breed, producing as few as 1.6 nestlings per successful nest. Nests with one and two young predominate, nests with three young are less common, and nests with four young simply do not occur. My food remains data indicate that the Snowshoe Hare is, in terms of biomass, the main food item found in Great Horned Owl nests in Saskatchewan in May (C.S. Houston and H.C. Smith, mss.). Even at the bottom of the hare cycle when we see no hares at all, the owls somehow find an occasional hare and bring it as food to their nest.

Figure 1 in fact minimizes the effects of Snowshoe Hare numbers on Great Horned Owl success,

since much of our overall Saskatchewan banding area contains both Jack Rabbits and Snowshoe Hares. The best Snowshoe Hare habitat within the aspen forest at Birch Hills - Crystal Springs - Yellow Creek - Cudworth - Humboldt - Wadena was therefore contrasted with a more southerly rectangle which includes Simpson - Raymore - Kelliher - Duval - Strasbourg - Bulyea. Because the northern area has so few nests at the bottom of the cycle, the long-term average number of successful nests there is only 19, as compared with the average of 30 further south. In a peak owl year of 1981, when hares were visible everywhere, the northern area had 42 successful nests -- which fledged 102 young owls. In 1985, when hares were nowhere to be seen, the last of two known incubating female owls was still on her nest on 9 May but had deserted by the time of our fruitless visit on 19 May.

In contrast, the southern area in the peak year of 1981 also had 42 successful nests -- which fledged 118 young. In 1985, at the Snowshoe Hare low, these owls had dropped to half their previous numbers and were apparently relying on Jack Rabbits, for there were 20 successful pairs able to fledge 37 young.

Finally, there was a highly significant correlation ($r=.61$, $p < .01$) between the number of nests found and the average number of young produced per successful nest. This offers further support for my conviction that cyclical variations

are real and not merely artefacts, for example, of observer effort.

DISCUSSION

Although the Great Horned Owl is a strong and capable hunter, food is very much restricted due to cold weather and deep snow during courtship in February and during incubation in March. In the aspen parkland of Saskatchewan, this owl's reproductive success depends heavily on its main prey species, the Snowshoe Hare. As a result, their cycles are closely synchronous.

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Reversed Size Dimorphism in 10 Species of Northern Owls¹

W. Bruce McGillivray²

Abstract.--Nineteen measurements were taken on museum specimens of 8 species of northern forest owls as well as two other common northern owls. Dimorphism indices were computed for all characters and combined with life-history data in a principal component analysis. Overall levels of SSD vary from 2.5% (Northern Hawk-Owl) to 8.0% (Boreal Owl). There are no relationships between SSD and migratory habitat, size, and higher order taxonomy of the species. Dimorphism levels are lowest for skull characters and highest for body core measures. For many characters, sexual size dimorphism is correlated with the percentage weight difference between males and females.

INTRODUCTION

Reversed size dimorphism (RSD) is said to occur if the female of a species is larger than the male. This situation obtains for most, but by no means for all, species of raptorial birds (Falconiformes, Strigiformes and Stercorariidae). These taxa are not closely related, therefore a unitary explanation for the evolution of RSD has not been possible. A wide variety of hypotheses have been proposed to explain RSD in diurnal raptors (see Mueller and Meyer 1985 for a recent review and references) although the relevance of many of these hypotheses for owls is debatable (Mueller 1986). Only Earhart and Johnson (1970) and Mueller (1986) have specifically examined the question of RSD in the Strigiformes (see also Snyder and Wiley 1976).

I showed for Great Horned Owls (*Bubo virginianus*) that the standard measures of size (weight and wing length) used in previous RSD studies are not highly correlated with multivariate estimates of size obtained from skeletal characters (McGillivray 1985). As well, the degree of RSD varied from -2.18% to 9.75% among the 16 skeletal characters. A

legitimate question is: which characters should be selected to give the best measure of the difference in size between males and females?

There are several assumptions with respect to size that are implicit in discussions of the evolution of RSD:

(1) Variable x (or y) is a good measure of size. It is assumed that we can measure some characters (e.g., wing length or weight) and using them to determine quantitative differences between males and females; relate these numbers to interactions between members of pairs which led to the evolution of RSD. The problem is as noted above - the choice of characters may affect the assessment of size variation. It is not easy to define size univariately since intercharacter correlations may be low. Consider the Great Gray Owl (*Strix nebulosa*), by wing length it is the largest North American owl but by weight it ranks a distant third behind the Snowy (*Nyctea scandiaca*) and Great Horned Owls (Earhart and Johnson 1970). Is the Great Gray therefore a large or a medium-sized owl?

(2) Correlations derived from interspecific comparisons are valid for intraspecific relationships. Figure 1 shows 2 variables, which are highly positively correlated if examined across a range of species but within each species they may be uncorrelated or even negatively correlated. These types of interspecies correlations lead to the concept that any of several characters is adequate for estimating size.

¹Paper presented at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

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Table 1.--Storer's index of dimorphism¹ for 17 skeletal characters of 10 species of owls. Sample sizes are in parentheses (no. of males/no. of females).

Variable ²	Nyctea scandiaca (16/22)	Bubo virginianus (53/79)	Strix nebulosa (25/49)	Strix varia (8/7)	Asio flammeus (51/32)	Asio otus (11/4)	Aegolius funereus (8/1)	Aegolius acadicus (8/9)	Surnia ulula (1/3)	Glaucidium gnoma (2/1)
skull	4.5	3.3	3.6	1.8	1.6	1.0	4.1	3.8	4.1	- 5.8
skull wid.	1.7	-2.2	3.2	0.5	1.4	-0.36	7.5	1.1	1.8	5.2
intorb. wid.	7.1	4.5	1.7	-1.3	0.9	1.2	3.5	1.1	-2.7	-15.6
mandible	5.2	4.4	2.8	1.2	2.5	1.4	5.3	2.2	5.3	- 6.3
coracoid	7.8	6.4	7.4	3.7	4.0	3.2	7.5	4.9	-1.9	2.4
sternum	6.8	5.6	7.6	2.0	4.2	3.5	9.2	2.2	1.8	2.9
Keel	5.5	5.4	8.3	-0.2	4.4	2.2	9.3	1.6	1.9	- 1.3
Sternum wid.	9.5	3.7	4.6	4.6	5.5	3.2	5.3	2.6	6.4	9.0
Humerus	8.3	5.7	6.6	3.1	3.8	3.0	8.5	6.0	1.5	3.8
Ulna	8.0	5.4	6.4	3.4	3.9	3.0	8.0	5.6	0.3	3.6
Carpomet.	7.6	5.4	7.0	4.3	3.3	3.4	9.6	5.6	0.5	6.5
Femur	7.1	4.1	5.7	3.0	3.4	2.7	9.7	4.8	1.1	6.1
Tibiotarsus	6.9	3.8	5.8	4.0	4.5	3.6	12.4	3.8	-1.0	4.8
Tarsomet.	7.1	2.3	5.4	3.6	4.8	2.7	8.7	2.3	-1.1	5.7
Tarsom. wid.	10.7	9.8	10.4	7.8	4.7	4.2	12.8	4.0	7.1	0.7
Synsacrum wid.	11.1	9.7	8.5	3.2	5.4	5.9	11.0	5.2	5.6	7.2
Scapula	10.2	6.5	7.3	3.8	4.8	2.5	11.4	4.3	4.8	3.4

¹ Negative values indicate that males are larger than females

² Variables represent maximum length unless otherwise indicated

(3) A "trait important in the evolution of RSD should be expressed to a greater extent in species with high RSD than in

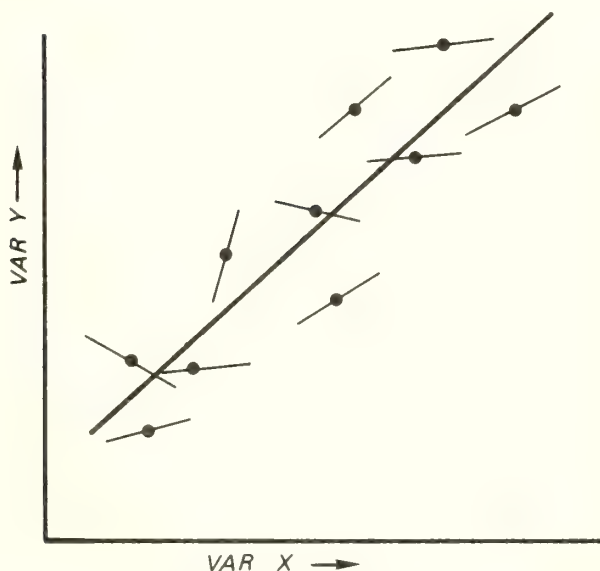


Figure 1.--Hypothetical relationship between x and y demonstrated interspecifically - solid line based on species means and intraspecifically - short lines. Note that the relationship holds interspecifically regardless of the slope demonstrated within each species.

those with low RSD." (Mueller 1986: 404). First, if RSD varies from one character to another, which is the best measure to test the trait against; and secondly, by choosing a particular measure of RSD, we are biasing our analysis in favor of traits which are related to this measure. For instance, if weight is the measure of RSD used, a correlation between intra-pair dominance and RSD in weight may be a strong argument for the significance of female dominance in the evolution of RSD. However, I would argue for example, that the lack of a correlation between diet and RSD for weight does not preclude a role of male/female diet differences in the evolution of RSD for skull or leg characters which may not be correlated with weight. Finally, this assumption precludes modification of the relative size of males and females which occur for reasons unrelated to the initial evolution of sexual size dimorphism (Johnston and Fleischer 1981, Payne 1984, Jehl and Murray 1986).

In this paper I look at RSD for 10 species of owls which occur in Alberta; 8 of these are northern forest owls. RSD is assessed univariately with skeletal characters and multivariately through character complexes. The purpose of the paper is to determine whether patterns for RSD exist both within and among species which can provide insight into the best methodology for estimating size and examining the evolution of RSD in owls.

MATERIALS AND METHODS

Data Collection

Nineteen measurements were taken with dial calipers on skeletons of 10 species of northern owl. Most measures defined a greatest linear dimension such as length or width of an element. A description of the measures (Table 1) can be obtained from Schnell (1970). Note that tarsometatarsus width (in this paper) equals the tarsometatarsus distal end width of Schnell (1970). Because some owl skeletons were prepared with the rhamphotheca removed and others with it attached, skull length and mandible length were defined as composite measures to standardize the data (McGillivray 1985). Hence, skull length equals total skull length minus premaxilla length and mandible length equals total mandible length minus dentary length. Most specimens are from the collection of the Provincial Museum of Alberta and were obtained in Alberta, Canada. However, some Pygmy Owls (*Glaucidium gnoma*) are from the state of Washington, some Hawk Owls (*Surnia ulula*) were obtained in Ontario and some Barred Owls (*Strix varia*) were acquired in several eastern states of the USA. To provide standard measures of weight, I used the values given in Snyder and Wiley (1976).

Data Analysis

RSD for skeletal characters was initially examined univariately using a dimorphism index (DI) of Storer (1966). The index measures the difference between the variable means of each sex (female \bar{X}_f ; male \bar{X}_m) as a percentage of the grand mean [$100 (\bar{X}_f - \bar{X}_m) / (\bar{X}_f + \bar{X}_m) / 2$].

Skeletal characters were grouped into "complexes" to facilitate interpretation of interspecific differences. The size of a complex equals the sum of the size of each variable in the complex. The sum of a group of characters represents a standard size axis (Mosimann 1970, Reymont et al. 1984) and is shown to be analogous to an ideal isometric size vector derived from a principal component analysis (McGillivray 1985, Somers 1986). The four complexes are skull (the sum of skull length, skull width, and mandible length); body (the sum of coracoid length, sternum length, keel length, sternum width, scapula length and synsacrum width); wing (the sum of humerus length, ulna length and carpometacarpus length) and leg (the sum of femur length, tibiotarsus length, tarsometatarsus length and tarsometatarsus width).

Relative trait lengths (Cherry et al. 1982) were calculated for the four character complexes and compared among species. These measures (which equal complex size/total size, where total size is the sum of all the

characters) although not statistically independent of size (Atchley et al. 1976, Somers 1986) provide a convenient method of comparing relative dimensions of characters between sexes of a species and among species for each sex.

Finally, the skeletal data generated in this study were combined with data presented in Mueller's (1986) discussion of reversed size dimorphism in owls in a principal component analysis. This analysis generated components linking diet, weight variation, clutch size and egg weight to RSD as measured by skeletal characters. All statistical analyses were run using the SAS statistical package (SAS Institute 1985) or with a hand calculator.

RESULTS

A summary of univariate measures of RSD for each species is given in Table 1. For all species, there is considerable intercharacter variation in the degree of RSD. It is also apparent that there is great variation among species in the degree of RSD for each character. This variation will be examined in greater detail later but it is worth noting two things here. First, intrageneric species pairs (*Asio*, *Aegolius* and *Strix*) show no greater similarity than intergeneric pairs. Secondly, the amount of RSD exhibited for coracoid, sternum, keel, and carpometacarpus length and tarsometatarsus width is significantly correlated with RSD for weight ($r=0.68, 0.71, 0.71, 0.63$ and 0.71 respectively, $P<.05, n=10$). RSD for humerus length and ulna is correlated at 0.61 and 0.62 respectively with RSD for weight, these are very close to the .05 level of 0.63 .

These data are more easily interpreted if the variables are combined into character complexes (Table 2). Overall, mean levels of RSD are highest for body characters and lowest for head characters (Table 3). There is no relationship between rank size (weight) and RSD for weight (Table 2). As well, all correlations between RSD for weight and RSD for character complexes are not significantly different from 0.0. Two potential sources of pattern in RSD variation are phylogenetic similarity and habitat preferences. However, none of the intrageneric species pairs show particularly similar levels of dimorphism. As well the two open-country and migratory species - *Nyctea scandiaca* and *Asio flammeus* show quite different levels of RSD.

A multivariate examination of RSD was made by including the univariate measures of dimorphism and those obtained from character complexes with variables given in Mueller (1986:392) in a principal component analysis. Variables taken from Mueller (1986) are wing loading, percent mammals, birds and

Table 2.--Dimorphism indices for weight and skeletal character complexes of 10 species of owls. Species are ranked (from left to right) by weight.

	Nyctea scandiaca	Bubo virginianus	Strix nebulosa	Strix varia	Asio flammeus	Asio otus	Aegolius funereus	Aegolius acadicus	Surnia ulula	Glaucidium gnoma
Head	4.1	2.4	3.0	1.1	1.7	0.36	4.9	1.9	2.9	-4.5
Body	8.3	5.7	7.4	2.8	4.7	3.4	8.9	2.9	2.5	5.2
Wing	8.0	5.5	6.6	3.4	3.8	3.5	8.2	5.8	0.8	4.2
Leg	7.2	4.0	5.9	3.8	4.3	3.1	10.8	3.6	-0.5	5.2
Weight	17.8	27.7	32.4	23.6	18.3	13.0	31.4	19.2	14.1	16.4

invertebrates in the diet, average clutch size and egg weight. A subset of the significant eigenvectors generated by the PC is shown in Table 4. PC1 clearly is an axis of RSD (for skeletal characters) since RSD levels for all four skeletal character complexes are significantly correlated with scores on PC1. The only non-skeletal variable to load significantly ($r > .63$) is percent weight difference (= RSD for weight). The only skeletal characters to load significantly on PCII are skull characters and these are associated (negatively) with percent mammals in the diet and (positively) with percent invertebrates in the diet. Figure 2 shows the position of the species on these 2 axes. They are well separated on PC1 but only *Glaucidium gnoma* is distinct on PC2.

It has been established here that females of these 10 species are generally larger than males for all 17 skeletal characters. It is useful to see if the relative size of skeletal characters (i.e., shape sensu Mosimann 1970) differs between the sexes. Table 5 gives relative trait lengths for character complexes. With few exceptions, females have relatively smaller heads, larger body cores and larger wings than do males. There are no obvious sexual differences in relative dimensions of leg bones.

The consistency of the shape differences between males and females suggests that shape changes may be associated with size and may not be related to sexual differences. To test this, I looked at the correlations between weight and relative size of character

Table 3.--Mean levels of sexual size dimorphism for character groups of 10 species of owls.

Character Group	Mean D.I.	S	N	t
Skull	1.79	2.58	10	2.19
Body	5.18	2.36	10	6.93**
Wing	4.69	2.36	10	6.29**
Leg	4.74	2.93	10	5.11**

** $P < .01$, t-test

complexes for each sex across the 10 species. Table 6 shows some consistent shape changes that are associated with weight differences among the 10 species. Therefore, regardless of sex, heavy owls tend to have relatively smaller heads, and relatively longer wing bones compared to lighter owls. The only male/female shape difference which does not seem related to size (weight) is the relatively large body core of females.

DISCUSSION

The concerns raised in the introduction over the choice of an appropriate character to measure RSD seem merited on examination of Table 1. The degree of RSD is quite variable among characters within each species. Combining characters into related complexes allows for reduction in the number of variables and should not obscure relationships

Table 4.--Significant eigenvectors¹ associated with a subset of the variables considered in a principal component analysis of skeletal sexual dimorphism, weight and ecological measures (from Mueller 1986).

Variable	PC1	PC2
Skull	0.64	-0.67
Body	0.92	--
Wing	0.92	--
Leg	0.86	--
Weight	--	--
Abs. wt. diff.	--	--
% wt. diff.	0.71	--
Wingloading	--	--
% mammals in diet	--	-0.89
% birds in diet	--	--
% inverts in diet	--	0.85
Clutch size	--	--
Egg weight	--	--

¹Eigenvectors expressed as the correlation between the original variables and the principal components.

Table 5.--Relative trait lengths of character complexes of owls [$= \sum X_{ij} / \sum \sum X_{ij}$, the sum of all characters (i) in complex (j) divided by the sum of all characters (all ij)]. Sample sizes are in parentheses (no. of males/no. of females).

	SKULL		BODY		WING		LEG	
	Males	Females	Males	Females	Males	Females	Males	Females
Nyctea scandiaca (16/22)	.170**	.165**	.307	.310	.324*	.326*	.213	.213
Bubo virginianus(53/79)	.179**	.175**	.280**	.283**	.302**	.305**	.256	.254
Strix nebulosa (25/49)	.201**	.195**	.279**	.283**	.305**	.307**	.246	.246
Strix varia (8/7)	.206	.202	.277	.276	.289	.290	.256	.258
Asio flammeus (51/32)	.179**	.175**	.281**	.284**	.314	.313	.241	.242
Surnia ulula (1/3)	.210	.214	.315	.319	.279	.275	.220	.216
Asio otus (11/4)	.197**	.193**	.273	.275	.301	.303	.249	.250
Aegolius funereus (8/1)	.252	.239	.296	.299	.258	.262	.226	.231
Aegolius acadicus (7/9)	.256*	.251*	.291	.290	.251*	.255*	.237	.237
Glaucidium gnoma (2/1)	.238	.225	.321	.322	.237	.243	.234	.238

* Difference between males and females significant at $P < .05$, t -test
 ** $P < .01$, t -test

since most characters in a complex are highly intercorrelated.

Table 2 shows no obvious patterns for these character complexes in the degree of RSD among species. Mueller (1986: 403) concludes that "the facilitation of female dominance is thus the most viable hypothesis on the evolution of RSD, in spite of the scarcity of data on dominance relationships." While I

Table 6.--Correlations between weight and relative size of groups of skeletal characters for male owls (above the diagonal) and for female owls (below the diagonal).

	Weight	Skull	Body	Wing	Leg
Weight	----	-0.73*	-0.14	0.73*	-0.03
Skull	-0.75*	----	0.31	-0.93**	-0.15
Body	-0.10	0.26	----	-0.49	-0.79**
Wing	0.76*	-0.92**	-0.44	----	0.13
Leg	-0.09	-0.09	-0.79**	.08	----

* $P < .05$
 ** $P < .01$

cannot comment directly on this hypothesis using data presented here, I would predict that closely related species would show similar male/female dominance relationships. Yet in this study, there was no tendency for congeneric species to show related levels or patterns of dimorphism.

The Snowy Owl and the Short-eared Owl are both migratory, open-country birds. They thus differ dramatically from the rest of the owls considered here which are relatively sedentary forest-dwelling species. Despite these major ecological differences, RSD values for Snowy and Short-eared Owls are very different and in no way distinctive from the forest-dwelling species. If these major ecological differences are not reflected in levels of RSD, how likely is it that subtle ecological factors such as: (1) variation in prey agility (Andersson and Norberg 1981, Safina 1984, Temeles 1985); (2) mode of nest defense (Wiklund and Stigh 1983); or (3) flight performance (Reynolds 1972, Andersson and Norberg 1981) are the key to understanding interspecific variation in levels of RSD.

Combining individual skeletal elements into groups is useful in comparing relative levels of dimorphism for different parts of

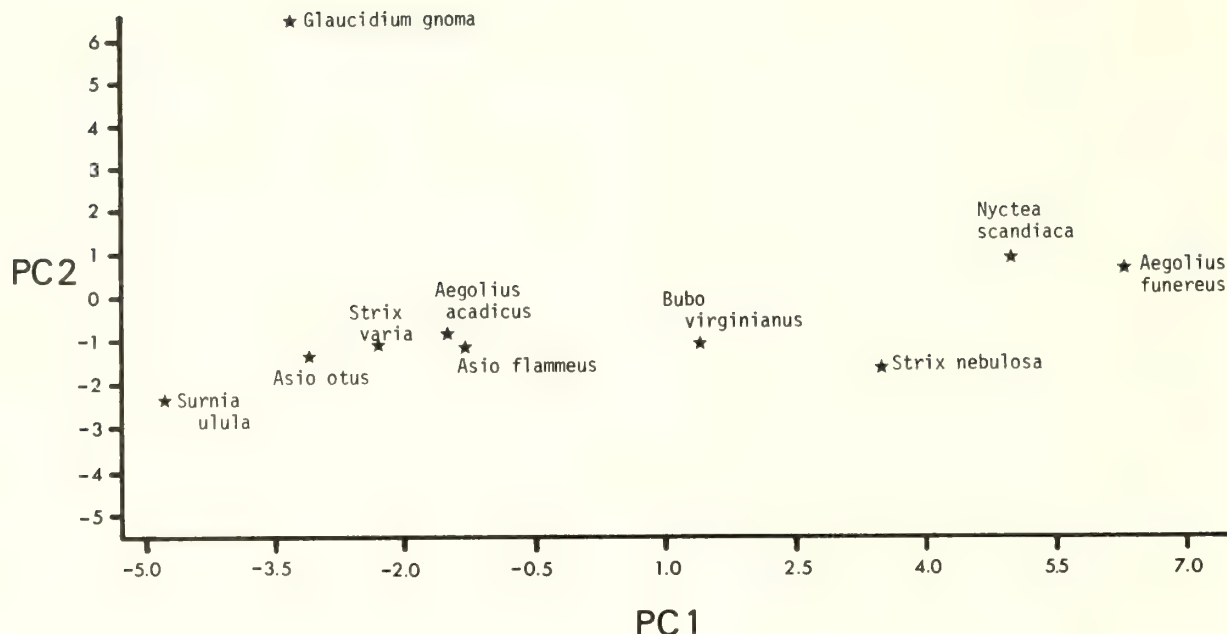


Figure 2.--Plot of species means on principal components 1 and 2 based on skeletal characters and a variety of ecological measures. PC1 appears to serve as an axis of RSD.

the skeleton. It is clear from Table 3, that skull elements are less dimorphic than either body core or limb elements. McGillivray (1985) suggested that relatively wide skulls in Great Horned Owl males might improve their ability to locate prey by sound. Evidence for this is not as convincing in other species with only *Asio otus* showing negative RSD (males larger than females) for skull width.

From a strict statistical standpoint, there was no correlation between RSD for character complexes and RSD for weight between males and females. However, I believe this is misleading because the correlation of body core characters and wing characters with RSD for weight are (.60) just below the .05 level of 0.63; and several component characters (coracoid, sternum, keel, carpometacarpus) show significant correlations. It would be very surprising from a theoretical standpoint to not find a relationship between skeletal dimensions and weight (Schmidt-Nielsen 1984). This relationship is further supported by the principal component analysis in which the only variable related to overall skeletal dimorphism was the percent weight difference between males and females.

The association on PC2 between low levels of skull dimorphism and a high insect, low mammal diet is intriguing but the plot (Fig. 2) reveals that this axis is created by *Glaucidium gnoma* which diverges dramatically from the rest of the species. Overall there is little support for the role of diet in modifying RSD which confirms Mueller's (1986) conclusion.

There are consistent shape differences between males and females of the species considered here. Males have relatively larger skulls but smaller body core and wing elements. However, Table 6 shows that these shape differences, with the exception of body core measures, are a function of size. In other words, there is no evidence for shape variation between males and females which is consistent with differing ecological roles. Table 6 (and 5) also indicate that despite their different habitat and behavior, these 10 species show virtually no shape differences other than those associated with size. The only exception appears to be leg elements where interesting variation is found. For instance the tarsometatarsus is very short in both *Nyctea scandiaca* and *Surnia ulula* relative to their overall size. The link between prey size, habitat, and climate and leg size in owls is worth further examination.

CONCLUSIONS AND RECOMMENDATIONS

The rank ordering of these 10 species by RSD as estimated on PC1 (Fig. 2) differs from the findings of Mueller (1986) and Earhart and Johnson (1970). However, in both these previous works the rank order depended on the variable used to measure RSD. For both studies, the correlation between RSD measured by wing and that measured by weight in North American owls is 0.78 ($n=18$, Mueller 1986; $n=26$, Earhart and Johnson 1970). This value is highly significant but it shows that only 61 percent of the variation in one measure can be accounted for by the other. Wing length

has been shown to be a poor measure of size in RSD studies (McGillivray 1985, Mueller 1986) and it was not considered here. Mueller (1986) concludes that weight is the best measure to use in estimating RSD. In this study RSD in weight is shown to be related to RSD for some body core and wing elements; although these correlations are generally weak. The question is: does adequate weight data on owls exist to continue using weight as an index of size? My assessment is no based on three considerations: (1) Wijnandts (1984) has shown that weights for female Long-eared Owls vary as much as 25% during the breeding season. Females gain considerable weight prior to and during incubation but lose it and more during the nestling period. Throughout this period, the female needs to remain mobile for nest defense and to escape predation, therefore the skeleto-musculature must be large enough to deal with the extra weight.

(2) Weight data obtained from museum specimens are biased because most owls are obtained as road kills or accidental casualties. These birds are often in poor condition when they died and weights are obtained after much dessication. As well for northern species, most individuals are acquired during migration or during southward movements in winter. Therefore, weight data are from outside the breeding season which likely underrepresents the extent of weight dimorphism (Wijnandts 1984, McGillivray 1985). An example from this study is for *Nyctea scandiaca*, for which virtually all specimens in North American museums are winter birds. The level of RSD for skeletal measures for Snowy Owls is very high (second only to *Aegolius funereus*) yet the level for weight is only 17.8% which ranks 3rd lowest among the 10 species. I would predict that weight dimorphism for Snowy Owls would be considerably higher than 17.8% if measured during the breeding season.

(3) All the weight data used are from one source. Mueller (1986) cites Dunning (1984) but Dunning obtained weights from Snyder and Wiley (1976) who used data from Earhart and Johnson (1970). For studies of RSD in North American owls, all the weight data originate with Earhart and Johnson (1970). Given our understanding of geographic variation in many species, and potential biases associated with museum specimens, a larger data base is required before we have adequate estimates of RSD in weight.

My recommendation is that attempts be made to obtain breeding season weight data such as acquired by Wijnandts (1984), but in lieu of that to use skeletal measures to estimate RSD. There is a good body of theory linking skeletal dimensions to mass (Schmidt-Neilsen 1984). Most skeletal differences between male and female owls examined here appear related to mass. A worthwhile area of study would be

an examination of the weight flux female owls undergo during the breeding season and how this varies among species. Selection for large size might occur if the female is required to gain considerable weight during incubation. If so, it may be necessary to reconsider the role of ecological factors in the evolution of RSD.

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Disease Susceptibility in Owls¹

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Abstract.--Disease may be a significant factor in the population dynamics of free-living species. Subclinical disease may alter food gathering capabilities, ability to escape predators and reproductive success. This paper describes three disease outbreaks in owls: Hippoboscids fly infestation, *Cyathostoma americana* (gapeworm) infestation and fungal pneumonia, (Aspergillosis) to illustrate that disease can impact recruitment and survivability of owls.

INTRODUCTION

Disease is any process which alters normal body function and results in decreased production and survivability. Disease may be caused by infectious agents, nutritional deficiencies or excesses, environmental toxins or genetic or congenital accidents. Studies in commercial livestock and zoological collections show that although some diseases may cause overt sickness and mortality most diseases are subclinical and interfere with either normal growth, behavior or alter reproductive success but do not necessarily kill the host. Commercial animal production industries go to great expense to monitor their animals for signs of subclinical disease which may affect the profitability of the enterprise.

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Naturally occurring disease is seldom considered to be an important factor in recruitment and livability of owls and yet in the present symposium data from several speakers showed survivability in young owls to be as low as 20% by the second year of life. "Starvation", "killed by a Great Horned owl", "fell from the nest site," eggs failed to hatch" were all given as reasons for mortality but complete post mortems were seldom performed to confirm the immediate cause of death or the presence of concurrent disease. It is possible that subclinical disease, whether due to hematozoan or ectoparasite infestation causing marginal anemia, neonatal bacterial diarrhea or septicemia, sublethal levels of a pesticide, or even limited prey availability causing subnormal growth efficiency may alter a young owl's ability to secure prey or render the owl more susceptible to predation. Factors which alter survivability during the first year of life are important and poorly understood pieces of the natural history puzzle of owls. The following examples of specific diseases in owls serve to illustrate some of the factors that may influence an owl's susceptibility to disease and further emphasize that disease can have a significant effect on survivability and recruitment.

Example #1

Biting flies of the family Hippoboscidae are common on birds of prey but are usually considered to be non-pathogenic commensals. In August 1983 a Hawk owl (*Surnia ulula*) kept in a captive propagation project was found weakened from anemia caused by a heavy infestation of blood sucking Hippoboscids. Examination of other owls in the collection showed that several species, in particular Great gray owls (*Strix nebulosa*) and Hawk owls, had significant numbers of Hippoboscids. Hippoboscids could be found firmly attached along the base of blood quills of remiges and retrices of affected birds. These observations led to a small study in 1984 to determine:

- (1) if northern owl species were particularly susceptible to Hippoboscid fly infestation.
- (2) if Hippoboscid flies caused anemia
- (3) if moulting patterns of the owls influenced severity of infestation.

In order to interfere minimally with the breeding project owls were handled only three times: during mid to late July, mid-August (peak of Hippoboscid infestation in 1983) and early October. At each handling birds were examined for Hippoboscids, a blood sample obtained from the ulnar vein for packed cell volume (PCV) and total plasma protein (TP) and the progression of moult documented.

Table 1 shows the distribution of species infested with Hippoboscid flies. Great gray owls and hawk owl harboured the largest number of flies but the Snowy owl (*Nyctea scandiaca*) had few flies. Packed cell volumes (table 2) decreased in August corresponding to the heaviest Hippoboscid infestation. As there were no parasite negative control owls in this study it was not possible to rule out normal seasonal fluctuations of PCV but species such as the Great horned owl (*Bubo virginianus*) and Barred owl (*Strix varia*) which harboured low numbers of Hippoboscids did not show an August decrease in PCV. Hippoboscid infestation appeared to be related to the moulting pattern of the bird (fig. 1). Hawk owls and Great gray owls were in heavy moult during the peak

Table 1.--Hippoboscid fly infestation in several species of owls.

Species of owl	Sample size	Number of flies (mean + standard deviation)	Observation date
Great gray	6	175 + 28	August 8
Snowy	4	6 + 5	August 23
Hawk	1	150 + 0	August 8
Barred	3	8 + 2	August 23
Great horned	1	30 + 0	August 23
	1	4 + 0	August 29
Short eared	3	47 + 16	August 23
	3	2 + 1	August 29
Long eared	1	40 + 0	August 23
	4	5 + 3	August 29

Table 2.--Hematology (Packed cell volume and total plasma protein) in owls before, during and after emergence of Hippoboscid flies.

Species of owl	Date	Sample size	PCV(%) mean + s.d.	T.P. (g/100ml) mean + s.d.
Great gray	July 5	8	44 + 4	4.2 + 0.5
	Aug. 15	6	32 + 8	3.5 + 0.4
	Oct. 3	12	38 + 5	4.3 + 0.5
Snowy	July 6	3	42 + 1	5.9 + 1.0
	Aug. 16	3	32 + 3	4.9 + 0.7
	Oct. 3	5	37 + 5	5.3 + 0.6
Hawk	July 30	2	40 + 1	4.0 + 0.5
	Aug. 15	2	33 + 2	3.8 + 0.7
	Oct. 4	5	46 + 7	4.5 + 0.4
Barred	July 30	3	34 + 3	4.7 + 0.5
	Aug. 16	3	36 + 4	4.8 + 0.6
	Oct. 6	4	41 + 3	5.1 + 0.5
Great horned	July 6	5	38 + 2	4.2 + 0.8
	Aug. 1	5	45 + 5	4.4 + 0.5
	Oct. 4	4	38 + 4	4.5 + 0.1

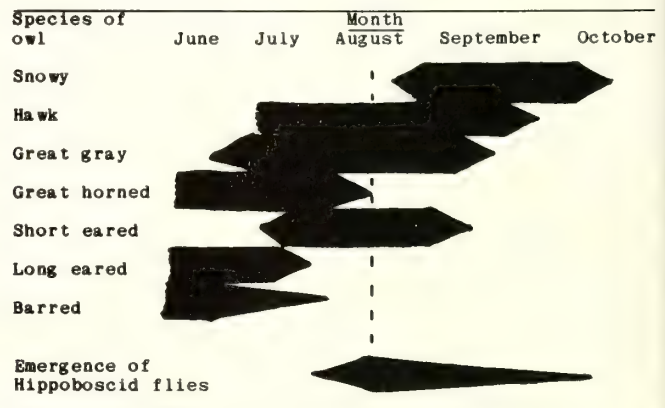


Figure 1.--Moulting pattern in owls, raised in a captive breeding project in southern Ontario, correlated with the emergence of Hippoboscid flies.

emergence of Hippoboscid flies. Owl species with fewer Hippoboscids appeared to be either finished their moult or as in the case of the Snowy owls not yet begun their moulting period. The feeding pattern of the Hippoboscid flies along the base of "in blood" feather quills supports the observation that birds in active moult are most heavily parasitised.

Example #2

Respiratory tract nematodes Syngamus sp. and Cyathostoma sp. have been occasionally reported from the respiratory tract of diurnal birds of prey (Chapin 1925, Bougerol 1967, Cooper 1985). In 1979 we identified Cyathostoma americana as the cause of death in a wild Saw whet owl (Aegolius acadicus) which had been admitted for trauma injury 10 days earlier. The following year Cyathostoma americana was responsible for the death of a hawk owl which had been maintained in captivity for several years. In 1986 Cyathostoma americana caused death in 5 of 13 juvenile Burrowing owls (Athene cunicularia) raised in a propagation release project in southern Ontario. Large numbers of worms were recovered from abdominal, cervical and clavicular air sacs, lung and primary bronchi from affected birds. All birds had severe airsacculitis and generalized necrotizing pneumonitis in response to aspirated nematode eggs and migration of adult worms (fig. 2). The original



Figure 2.--Lung of Sawwhet owl with a heavy infestation of the nematode Cyathostoma americana.

source of the parasite for this Burrowing owl colony is unknown but the owls have access to both earthworms which may act as intermediate host and to shrews (Blarina brevicauda) and star-nosed moles (Condylura cristata) which may act as paratenic hosts. Control of the parasite was accomplished by antihelminthic therapy combined with management changes aimed at controlling earthworms. In late 1986 a wild eastern Screech owl (Otus asio) was admitted to the clinic for traumatic injury and died within a few days with massive parasitic pneumonia caused by Cyathostoma americana.

Example # 3

Aspergillus fumigatus causes respiratory disease in all birds of prey. Clinical disease is usually a result of massive exposure of Aspergillus spores or the bird being immunosuppressed from some concurrent disease process or other stressors. In our experience at both the Ontario Veterinary College Wild Bird Clinic and the Owl Rehabilitation and Research Foundation northern owl species such as the Snowy owl, Great Gray owl and Boreal owl (Aegolius funereus) are very susceptible to Aspergillosis compared to more southernly species. These northernly species usually present with acute, fulminating Aspergillosis with massive fungal growth, invasion of blood vessels, lungs and other body organs rather than the more chronic localized lesions found commonly in more southernly owl species.

DISCUSSION

The three examples of disease in this paper were chosen to illustrate the complexity of host/parasite interrelationships. In order for disease to occur it is necessary to have a susceptible (non-immune) host, a pathogenic (disease causing) organism and an environment suitable to allow the host and disease causing agent to interact. The Hippoboscid infestation revealed that under certain environmental conditions an organism normally considered to be a commensal can cause anemia or even death. In this case the critical

environmental factors included the emergence of the Hippoboscids flies and the timing of the seasonal moult of the birds. Most of the owls developed a marginal anemia during the period of infestation. It is interesting to speculate whether a similar mild anemia in a wild owl would decrease food gathering ability or increase susceptibility to predation. Many raptors presented to our clinic have a marginal anemia and moderate to low levels of blood parasites, particularly Hemoproteus sp. and Leucocytozoon sp. As these agents are transmitted by biting arthropods it would be interesting to study nestling owls which are commonly infested with mosquitoes or black flies to determine if parasite induced hematologic changes may correlate with fledgling survivability.

The death of the captive Burrowing owls and the wild Sawwhet and Screech owl indicate that Cyathostoma americana is a potential pathogen. The high mortality in the Burrowing owl colony was undoubtedly related to housing and confinement of the birds; however, identifying Cyathostoma as the cause of death in wild Ontario owls raises questions about the significance of this parasite in owl species which feed on earthworms, shrews or moles.

Aspergillosis is well described in many avian species. Our experiences have shown that northernly species such as the Snowy owl, Hawk owl, Gyr falcon (Falco rusticolus), Rough-legged hawk (Buteo lagopus), Eider duck (Somateria sp.), Old Squaw duck (Clangula hyemalis) are very susceptible to fungal infections. This may be due to a lack of exposure to fungal spores in their home environment, to immunosuppression from migratory stressors, nutrition changes or stresses within our hospital environments. There have been no

studies to investigate comparative immune responses among species of owls.

In summary disease processes may affect species population dynamics in more subtle ways than killing the host. Subclinical disease may be an important factor in reproductive success and livability of wild owl populations. Our knowledge of naturally occurring disease in owls is very limited and it would be highly desirable for field biologists and veterinary pathologists to develop cooperative studies to investigate this fascinating aspect of owl biology.

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The Role of the Whitefish Point Bird Observatory in Studying Spring Movements of Northern Forest Owls¹

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Abstract.--The Whitefish Point Bird Observatory has had a spring owl banding program since its formation in 1978. Barred, Boreal, Great Horned, and occasionally Great Gray Owls are captured, in addition to the normally migrant Long-eared and Northern Saw-whet Owls. Thus, the observatory plays an important role in studying northward movements of many northern forest owls which move south out of the boreal forest during the winter. I summarize the 1978-1986 owl banding data and briefly explain future objectives for the observatory's owl banding program.

INTRODUCTION

The presence of significant numbers of owls was first noted at Whitefish Point, Chippewa County, Michigan during the spring of 1966 when mist nets set up to capture Sharp-shinned Hawks (*Accipiter striatus*) were left open at night. From 1966 to 1970, 280 owls of 6 species were banded at the point (Kelley and Roberts 1971). From 1971 to 1977 limited owl banding was done at the point, usually for only a couple weeks each spring. In 1978 the Whitefish Point Bird Observatory (WPBO) was formed and owl banding coverage improved dramatically as a result. In this paper I will summarize owl banding at WPBO from 1978-1986 and mention some studies that are currently underway.

METHODS

Because WPBO's banding program relies strictly on volunteer banders, it was not possible to have coverage

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for the entire spring. Banding coverage varied as follows: 2 wk in 1978; 2.5 wk in 1979; 6 wk in 1980-1983, 1985-1986; and 5 wk in 1984. The last week of April and the first week of May had coverage during all years. The earliest coverage ever began was the last week of March (1981 and 1983) and the latest it continued was through 9 June (1982).

Six to 22 mist nets were operated during the periods of coverage. The number of nets depended on the number of banders present and their levels of experience. During the first 4 years both 61 mm and 121 mm stretched mesh mist nets were used. From 1982-86 almost all nets used were 121 mm stretched mesh. Accurate net hour information, the locations where nets were placed and the net locations where owls were captured were not regularly recorded until 1984.

Luring for larger owls (Great Horned, *Bubo virginianus*; Long-eared, *Asio otus*; Barred, *Strix varia*; and Great Gray, *Strix nebulosa*) with pigeons and starlings took place at dusk during a few nights most years, usually during April. Birds were either lured into mist nets (Grigg 1975) or were captured with bownets when they bound to the lure bird.

During 1980, 1983 and 1984 a few owls were also captured with 3 to 6

Table 1.--Numbers of owls banded at Whitefish Point Bird Observatory, 1978-86.

<u>Species</u>	<u>1978</u>	<u>1979</u>	<u>1980</u>	<u>1981</u>	<u>1982</u>	<u>1983</u>	<u>1984</u>	<u>1985</u>	<u>1986</u>	<u>Total</u>
Great Horned Owl					1	15	36	5	10	67
Barred Owl	3	4	3	2	11	4	38	3		68
Great Gray Owl			2	1		1	11	3	1	19
Long-eared Owl	24	23	29	144	18	24	23	20	49	354
Boreal Owl	23	7	2		36	18	47	5	1	139
Northern Saw-whet Owl	18	20	25	50	23	77	63	38	93	407
										1,054

automatic bownets baited with mice, pigeons and starlings.

RESULTS AND DISCUSSION

There have been 1,054 owls of 6 species banded since WPBO was formed as summarized in table 1. The first owls are usually captured during late March to early April (table 2). Movements continue well into May during some years and at least into early June for the Northern Saw-whet Owl (*Aegolius acadicus*). Nights with heavy movement (10 or more owls/night) can occur anywhere from mid April to mid May and are very variable and unpredictable. During some years there are several nights with heavy movement and during other years there is never even a single night with heavy movement.

Except for some of the Northern Saw-whet and Long-eared Owls, most if not all of the owls captured are probably non-breeding individuals as breeding birds

Table 2.--Earliest and latest capture dates for owls banded at Whitefish Point Bird Observatory, 1978-86.

<u>Species</u>	<u>Earliest</u> <u>Capture</u> <u>Date</u>	<u>Latest</u> <u>Capture</u> <u>Date</u>
Great Horned Owl	25 Mar	25 May
Barred Owl	27 Mar	21 May
Great Gray Owl	10 Apr	21 May
Long-eared Owl	3 Apr	5 Jun
Boreal Owl	7 Apr	27 May
Northern Saw-whet Owl	1 Apr	8 Jun

would already be on their breeding territories prior to the initiation of our banding operations (see breeding dates in Bent 1961, Adamcik et. al. 1978b, Bondrup-Nielsen 1978, Nero 1980).

Since it has only been from 1984-86 that capture effort has been quantified, I will not attempt to make any detailed analyses of the numbers captured each year. However, enough coverage was available each year to make some gross interpretations of the data.

Long-eared and Northern Saw-whet Owls are the only species that are captured in good numbers every spring. The numbers of Long-eared Owls banded are usually fairly constant, though 1981 was a year they were exceptionally abundant. WPBO is currently studying sexing methods for this species. The numbers of Northern Saw-whet Owls appear to fluctuate more widely but since capture effort was not quantified for most years, comparisons between years would be meaningless. Weather (Mueller and Berger 1967, Evans 1980, Weir et. al. 1980) and the proportion of juvenile birds (Weir et. al. 1980) significantly affect numbers captured for this species in fall movements. WPBO is currently studying the effects of weather on the numbers of owls captured. Aging this species is much more difficult in spring than in fall; therefore, we have not been able to examine whether the proportion of juveniles to adults varies much from year to year. We hope to be able to address this question in the future as more of our banders become experienced at aging this species.

The numbers of Boreal Owls (*Aegolius funereus*) appear to be cyclical, with good numbers being present for 3 years followed by 2 years of few or no birds. However, more years of data will be necessary to

confirm this pattern. WPBO appears to be the best place in the United States to study the magnitude of southward movements of this species. Boreal Owls are seldom captured during fall (Evans and Rosenfield 1977) and apparently do not usually leave the boreal forest until winter is well underway. WPBO captures birds returning north in the spring so that the relative numbers of birds that left the boreal forest the preceding winter can be evaluated. It is interesting to note that even when this species does come south of the boreal forest it is sometimes not detected. In 1983 we captured fairly good numbers of Boreal Owls and there were no reported influxes for the winter of 1982-83 (Powell 1983, Weir 1983). WPBO is currently studying sexing methods for this species and we hope to be able to evaluate the age and sex composition of future influxes.

The numbers of the larger owls (Barred and Great Gray) banded prior to 1982 cannot be compared with later years due to extensive use of 61 mm stretched mesh mist nets during significant periods of banding coverage from 1978 to 1981. The 61 mm nets do not effectively capture large owls.

The number of Barred Owls appears to fluctuate considerably. This species was exceptionally abundant in 1984 and none were captured during 1986 even though there was excellent banding coverage during this year. The spring of 1984 was preceded by a large invasion of Barred Owls into Minnesota (Powell 1984) and Ontario (Weir 1984) during the winter of 1983-84. Whether this species fluctuates in a predictable cyclical fashion will require more years of data.

Great Gray Owls are captured in small numbers during most years. In the spring of 1984, which preceded a huge invasion by this species into Manitoba (Nero et. al. 1984), Ontario (Weir 1984) and Minnesota (Powell 1984) during the winter of 1983-84, more than usual were banded. Not enough years of data are available yet to examine cyclical fluctuations in this species.

Great Horned Owls are seldom successfully captured in mist nets. Thus, luring and trapping with automatic bownets provide the best methods to assess the occurrence of this species. The 10 year cyclical pattern of southward movement out of the boreal forest has been well documented for this species (Keith 1963, Adamcik et. al. 1978a, 1978b, Houston this symposium). The springs of 1983 and 1984 followed such invasions (Powell 1983, 1984; Weir 1983, 1984) and our data show that this species was abundant in these years. However, we

usually captured some Great Horned Owls each year that an effort was made to do so (1982-86). We plan to make luring a routine part of our banding operation so that we can better study movements of this species.

Three owls have been captured in subsequent springs- a Boreal Owl 2 years after initial banding (Carpenter 1985) and 2 Barred Owls a year after initial banding.

Some owls are recaptured again one or more nights following the initial date they were banded. All of the Long-eared and Northern Saw-whet Owls and most individuals of the other species were recaptured within a week of the initial banding date. However, 5 Barred Owls were recaptured 8 to 17 nights after their initial banding date, 3 Great Gray Owls were recaptured 13 to 24 nights after their initial banding date, 4 Boreal Owls were recaptured 14 to 29 nights after their initial banding date and a Great Horned Owl was recaptured 16 nights after the initial banding date.

In summary, WPBO is a unique spot for studying the northward movements of northern forest owls that moved south of their breeding range in the boreal forest during the preceding fall and winter. In addition to the annually migrant Long-eared and Northern Saw-whet Owls, we also are able to study Boreal, Great Gray, Great Horned and Barred Owl movements. In future years we plan to better quantify capture effort so that comparisons from year to year will be more meaningful.

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Reintroduction of the Ural Owl in the Bavarian National Park, Germany¹

Wolfgang T. Scherzinger²

In the mountains of the Bavarian Forest an isolated population of Ural Owls became extinct in the beginning of the 20th century. Reintroduction trials were started in 1972 by building a breeding stock, releasing zoo-born owlets, monitoring them with radio transmitters, and studies of habitat preference. A total of 123 owls were bred in captivity; of 76 released in the field, 10 were found dead. Only 5 birds have settled in the area. Problems occurred with risk of hybridization with the Tawny Owl (*Strix aluco*), long-distance dispersal of young owls, and low prey abundance during severe winters.

INTRODUCTION

Strix uralensis is a big, long-tailed wood-owl, with small black eyes, and radial marks on the facial disk; its body and head are heavily streaked, and it has broadly barred tailfeathers (fig. 1). (The German name "Habichtskauz" suggests convergent characters with the Goshawk).

In the Bohemian Forest, which reaches along the border from Bavaria/Germany (Bavarian Forest) through Austria to Czechoslovakia, the Ural Owl existed until the beginning of the 20th century. Actual knowledge is based on nesting records, shootings, and from taxidermists' reports. Only in Schwarzenbergs principality, in the area of Schattawa, were these owls monitored more systematically to the end of the last century (Wust 1986). Detailed data on population levels, abundance, or habitat choice are totally lacking. The last records are from 1926 (Kucera 1970; fig. 2).

The main distribution area of this species is to be found in Scandinavia, Siberia, and reaches to Japan. In the montane regions of Central and Eastern Europe, isolated populations have remained from the post-glacial period. Some journeys were made to study recent habitats of the subspecies *Strix uralensis macroura* in Czechoslovakia. This also occurred in the Bohemian/Bavarian Forest (fig. 3). In Eastern Slovakia, the Ural Owl lives in old mixed forest in lower montane areas with

oak trees or beech and fir. For breeding it primarily uses large Goshawk nests (Danko and Svehlik 1971).

THE PROJECT

In 1972 I was asked to develop a breeding project for a reintroduction experiment. Altogether we established five breeding pairs (the owls came from Sweden, Russia, Czechoslovakia, and

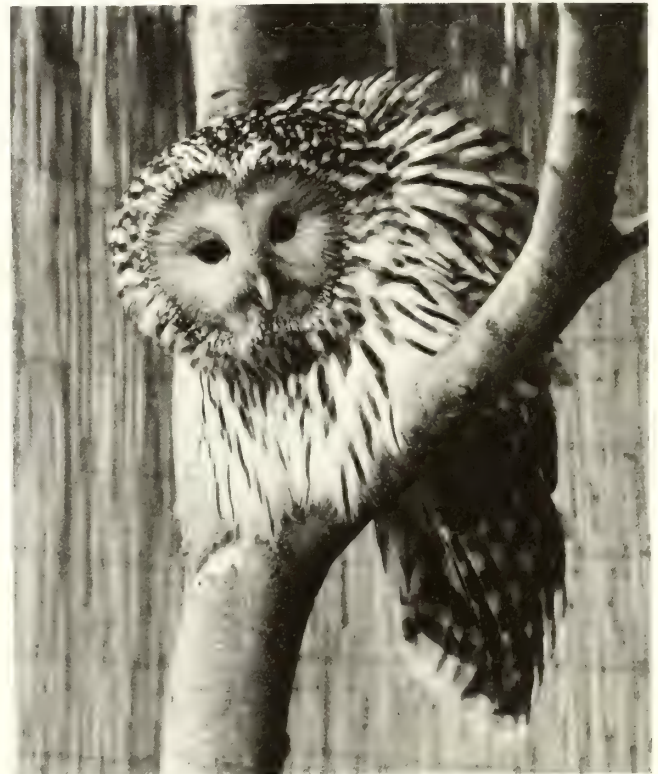


Figure 1.--An aggressive male Ural Owl.

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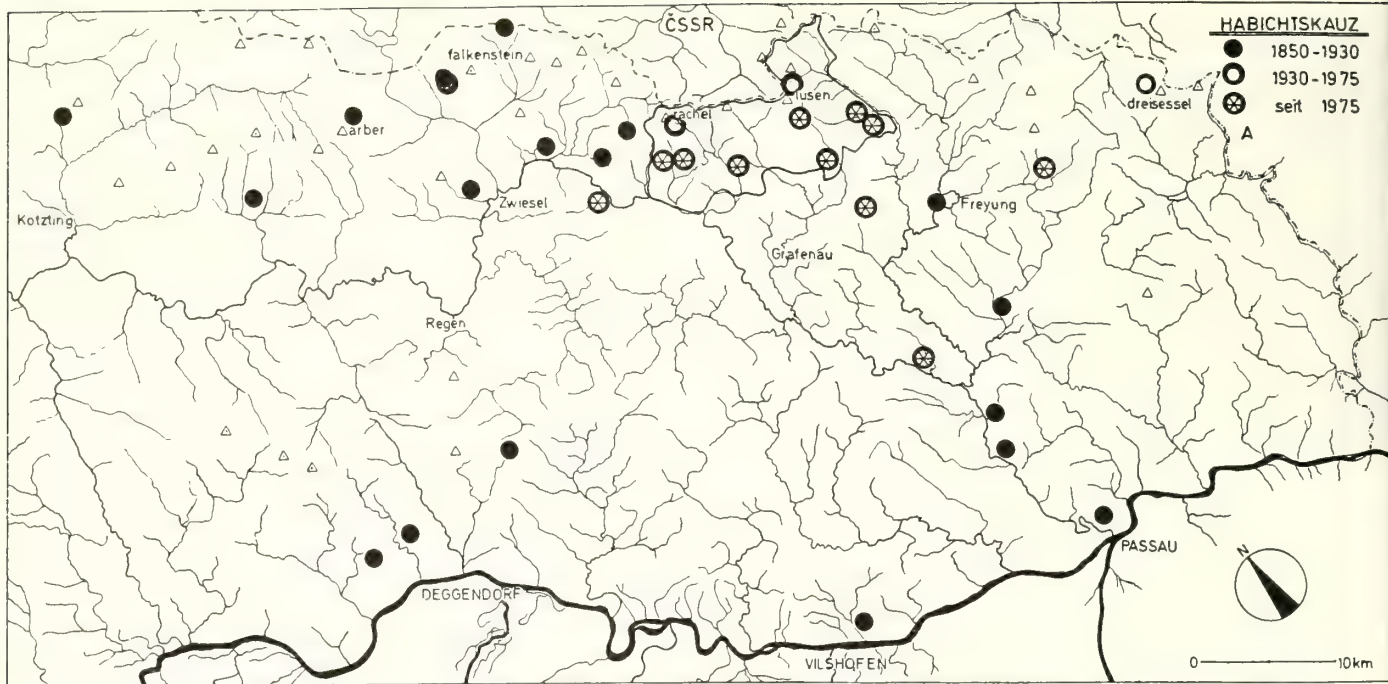


Figure 2.--Historical Ural Owl records in Bavarian Forest.

Yugoslavia, mostly from zoos). Fourteen of our offspring were offered to private breeders and zoos with the aim of founding a breeders association for this project. Between 1973 and 1986 an average of 2.5 eggs were laid per initiated brood ($n=60$), which means 2.7 eggs per clutch. Egg-laying started, on the average, on 21 March; re-nesting occurred until the beginning of May. Altogether 97 owlets were born (mean value = 1.7 nestlings per brood; 9x1, 12x2, 12x3, 7x4 young). Three died, so the final breeding success was 94 fledglings (Scherzinger 1974, table 1).

This success was the result of very good breeding conditions. Individual pairs were kept in aviaries measuring at least 4 by 8m, with large nestboxes (30 by 30cm base). We fed only freshly

killed mice and rats from the breeding farm (no chickens and no frozen food). The aviaries were situated in optimal habitat, each 1 to 3 km apart, so the young owls could be released right there.

For the reintroduction experiment we got 94 young from our breeding stock and 29 from the breeders association, for a total of 123 in 12 years. Seventy-six owls were released in the field, and 47 were kept in stock or given to breeders.

We have learned much about releasing techniques with the Eagle Owl project in our national park (Scherzinger 1987), and have also gained essential ontogenetic data from the breeding results in captivity (fig. 4). Young *Strix uralensis* are fully able to fly within 40 days; they change to adult plumage when 10 weeks



Figure 3.--The smooth mountains of Bavarian Forest national park are totally covered by woodland (photo: H. Strunz).

Tab. 1.-- Success of breeding Ural Owl in captivity (1973-1986).

breeding stock	1-5 paires in nationalpark 1-4 paires in breeders ass.
egg-laying starts	Ø March 21 (1.3.-1.5.)
clutch size	Ø 2,5 eggs /init. brood 2,7 eggs /clutch
youngs hatched	97 1,7 young/brood ($n=57$)
youngs grown up	94 1,6 young/brood 2,5 young/successf.brd.
youngs breed.ass.	29
reproduction total	123
breeding stock	22
Ural Owls total	145 ex.

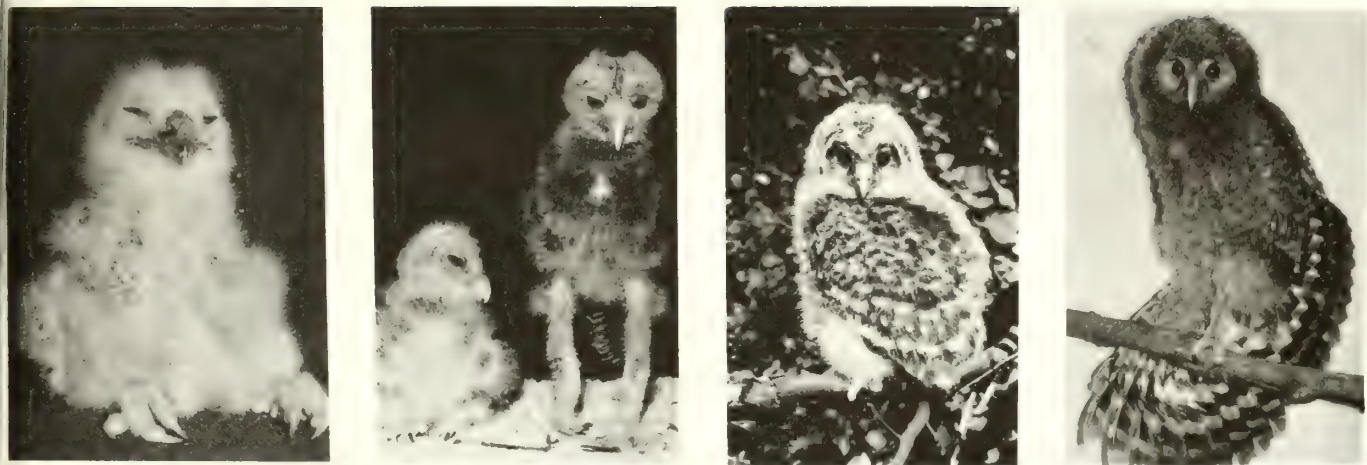


Figure 4.--Ontogenetic development of Ural Owl: 2, 16, 30, and 45 days of age.

old; the begging period ends during their 3rd month of life. The behavior for catching prey does not need to be learned (Scherzinger 1980). It is not necessary either to train the owls with live prey, if they have the opportunity to frequent a feeding place in the field. Ural Owls are most aggressive hunters, and feed on their own prey a few days after release.

The best age for setting them free is between 100 and 120 days. In this ontogenetic stage, plumage of adults is fully developed, the family context loosens, and the young owls are able to catch prey independently. During release, avoidance of stress or shock must be considered. Therefore it is necessary to do all the measurement, banding, and mounting of radios at least 3-5 days before release, so the birds have time to reassure themselves. They should be released at early dawn on days without wind or precipitation.

The young should be released beside the caged parents. When I put them into a small basket made from fresh branches outside the aviary, the owls free themselves by climbing out after a few minutes. Usually they spend their first night in a tree above the aviary in contact with the adult owls and brothers and sisters. A supply of known food is laid out daily within sight. The owls learn this place quickly. I will emphasize that offering food will not lead to dependence of the birds; they visit the feeding station only if they are unsuccessful in catching their own prey.

MONITORING

As long as the young owls utter begging calls, their position can easily be located. But just at the age of release the social family context breaks up and the offspring will disperse. I have not yet been able to develop an optimal technique to register systematically the daily locations of the birds. Owls found dead or observed incidentally give us hints on their fate.

Of 76 released birds, 10 were found dead (table 2). The lifespan of these owls has averaged only 6 months. This suggests that the mortality rate is highest at the end of winter, when body condition is at a minimum (extreme data: 46 days to 5 years). Most of the young owls disperse in autumn before snow cover decreases prey abundance. The average dispersal distance is 10.2 km (extreme data: 2 to 21km).

The recovery rate is surprisingly low (13%). This is on the one hand a fact of difficulty of survey in dense woodland, and on the other hand of unapproachable areas, especially in adjacent Czechoslovakia.

As the records of owls in the woodlands remained unsatisfactory, we have used radio transmitters from "Biotrack" (R. Kenward/GB), weighing 12g, working for 9-12 months and at a distance of 1-5km (fig. 5). As the "rucksack" package could affect the owl's prey-catching success, and the bird cannot get rid of the harness after the transmitter fails, we decided to mount radios on the quills of the middle tailfeathers. In this type of radio, the flexible antenna is fixed along the quills. This method has been demonstrated by Kenward (1978) with the

Tab. 2.-- Reintroduction of Ural Owl; release and recoveries (1973-1986).

release in 12 years	76	6,3 owls/year (extr.= 0-14)
found dead	10	13%
causes of death	3	starved
	2	fence
	1	traffic
	1	power line
habitat chosen	4	old mixed forest
	2	forest edge near meadow
distance of dispers.	Ø 10,2 kms	(extr.= 2-20kms)
age of recoverie	Ø 6 months	(extr.= 5 years)
telemetric equippm.	19 ex	in 4 years

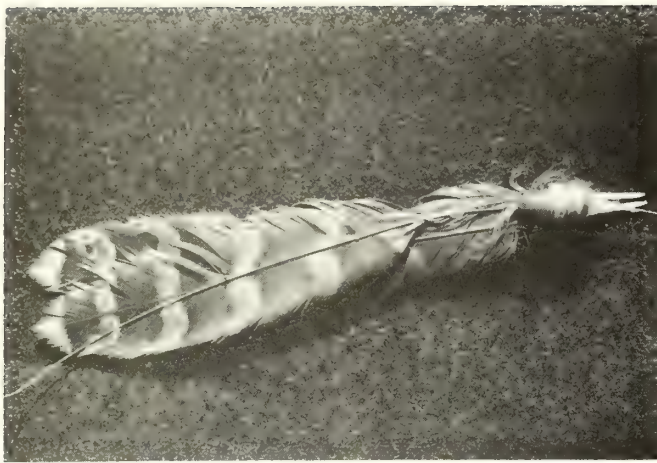


Figure 5.--Tail-mounted radio transmitter dropped after summer moult.

Goshawk, and we believe it would also be the safest technique for the Ural Owl, because the transmitter will drop with the tailfeathers during the yearly moulting. (Only 1 of 19 radio-marked owls pulled out the transmitter with its own tailfeathers, while entangled in a wire fence.)

We learned by telemetric techniques that the owls were very active during the first weeks after release. They flew 2-3km per day, also in bright daylight. After some weeks many of them had left the study area and we could no longer pick up their radio signals, especially when they went into Czechoslovakia. At the beginning of November the rest of the owls established home ranges in the national park, where they were frequently located, even after being absent for a few days.

When the daily locations are analyzed to characterize habitat preference of *Strix uralensis* in this region, the pattern is: warm slopes with mixed stands of old woodland (spruce, fir, beech, maple; fig. 6). The owls use elevations of 750 - 1000m above sea level mostly. Proximity to meadows and clearings is conspicuous. Single

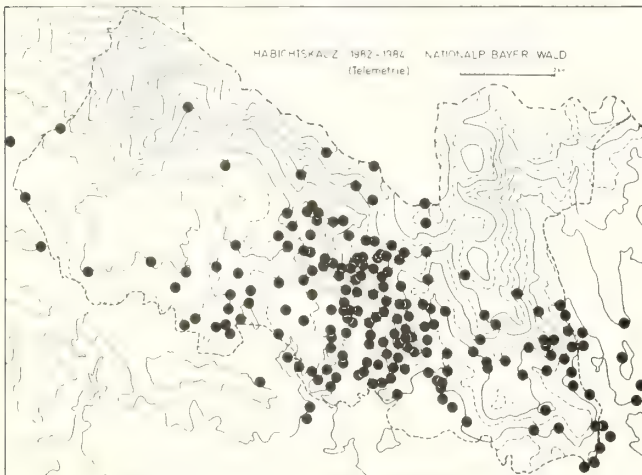


Figure 6.--Habitat preference shown by telemetric monitoring in the national park.

birds occupy surprising large areas. Maximum distance of individual locations was 12km for instance during early autumn dispersal, and almost 4km from an adult territorial female. It is an interesting fact that some owls re-occupied locations of former distribution in the Bohemian Forest, where the species was last recorded 50-60 years ago (Kucera, pers. comm.)!

In case the captive-bred owls could be imprinted to artificial nestboxes, I mounted 50 nestboxes of the same type as in the aviaries in suitable habitat. This could be another chance to raise the quality of monitoring, especially for breeding activity.

SUCCESS

Preliminary success of the reintroduction experiment can be sketched only in a rough way, as many released owls left the study area and only a few individuals provided good data. At least 5 individuals settled in the national park. Some home ranges were occupied over 5-10 years. Four clutches of two eggs each were found in the nest boxes (1983=1, 1985=2, 1986=1), but all the breeding was done by females without mates (fig. 7)!

Preliminary results indicate that males disperse over a larger distance than females (only 1 male was found to stay for over one full year), and that females can occupy a territory themselves, defending it by uttering territorial calls; they even start to breed there unpaired!

The main problems of this project can only be answered partly: a) It still is not possible to reconstruct causality of regional extinction: Was it caused by changes in forest harvesting? Did the shifting of climate from a continental to an atlantic type with more precipitation in 1920 - 1950 affect the birds? Was shooting a dominant factor? Was genetic isolation a problem in this local population when it separated from the main

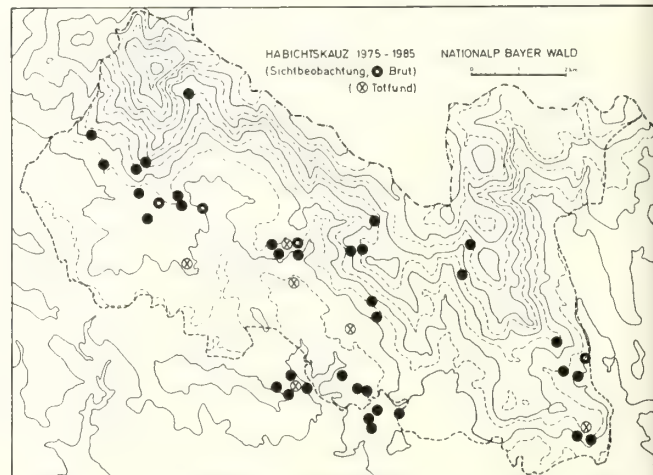


Figure 7.--Distribution of the Ural Owl in the national park, and locations of initiated broods.



Figure 8.--Natural forest is the objective of environmental development in the national park. Will this decrease habitat quality for the Ural Owl?

part in Eastern Europe? Was a separate, self-sustaining population established, or just a peripheral branch in the Bohemian Forest?

b) It is not possible to deduce data on former habitat characteristics from historical records. Until the beginning of the 20th century, for instance, heavy logging led to large clearcuts. In Scandinavian habitats the positive effect of large clearings in the forest is clearly shown for population trends of mice and Ural Owls. Today we try to reach quite the opposite objective through natural development of old, virgin woodland in the national park (fig. 8). The Ural Owl probably is dependent on open areas and cannot live in dense woods (?). Perhaps national park strategies will decrease quality of habitat in its woodland for this owl species.

c) The study area in the national park is 130km² and covers the montane and subalpine region of these mountains (about 700 - 1400m NN), for which heavy precipitation and long-lasting snow cover are characteristic (snow cover lasting from early November to April/May; depth of snow 80cm in the valleys and up to 250cm in the mountains). There the feeding situation will be adverse for birds of prey in winter. They probably migrate to lowlands with milder climate.

d) As far as we can conclude from breeding experiments in captivity, there is no genetic barrier against hybridization with *Strix aluco* as sibling species. This native owl species is common in the national park, with an abundance of 25 breeding pairs, on the average. Lacking a partner of its own species could stimulate the Ural Owl to choose the wrong mate!

Testing the risk of hybridization, I first reared Tawny Owls imprinted by Ural Owls as foster parents. When adult, such owls chose the foster species as social partners, but only birds from



Figure 9.--F1 hybrids of *Strix aluco* x *Strix uralensis*.

their own species as sexual partners, which they can recognize from the species-specific song. In contrast, normally reared Tawny and Ural Owls paired easily when lacking a partner of their own species. From this F1 brood, 3 hybrids were born; 1,1 young survived and the male was back-crossed successfully with Tawny and Ural Owls. The female showed full breeding behavior, but never laid an egg. Characteristics of plumage follow intermedial heredity (fig. 9), whereas voices are dominated by the Tawny Owl (matrocline? Scherzinger 1983). No records of hybrids exist from the field so far. The most important barrier for species isolation should be the specific voice, therefore.

e) The number of owls released annually was relatively small (6.3 owls per year). Consequently there was no realistic chance to get the area fully covered with good pairs.

f) There is a great risk of genetic isolation of the very small population which could be found in the national park. Following calculation of population genetics, a founder group of 20 specimens could be sufficient, but final abundance must rise to at least 500. Only 6 to 8 pairs of Ural Owl could be estimated to breed in the national park area. All the suitable habitats of Bohemian Forest, which lie in Bavaria, Austria, and Czechoslovakia, would be necessary to establish a stable population.

CONCLUSION

From preliminary experiments we can conclude that the Ural Owl can still exist in these mountains. Experienced individuals can survive

even under severe winter conditions, when there is heavy snow cover. In the future it will be necessary to release at least 15 - 20 individuals per year, probably from more wide-spread locations, to compensate for dispersal movements. Therefore we must create a larger breeding stock, either by enlarging the breeders association in cooperation with zoos and pet lovers, or by

enlarging our breeding station in the national park. This second way is very expensive and has been cancelled by our office this year. Therefore the resumption of reintroduction of the Ural Owl in the Bavarian Forest is at stake. The final decision will depend on results of an intensified monitoring project of radio-marked owls during the next years.

Mate and Nest-Site Fidelity in Ural and Tawny Owls'

Pertti Saurola²

Abstract.--This study is based on Finnish ring recoveries and retraps. The data suggests that 98-100% of Ural Owl (*Strix uralensis*) males, 90-95% of the females, and 80-90% of both sexes of the Tawny Owl (*Strix aluco*) are faithful to their previous nest site. Fidelity to the mate seems to be almost absolute (95-97%) in the Ural Owl, but less (80-85%) in the Tawny Owl.

INTRODUCTION

Owls are very popular among the subjects for Finnish bird ringers. More than 12 500 nest-boxes for owls and 3500 natural holes are checked annually (Haapala and Saurola 1986), and more than 10 000 owls were ringed in 1986, the top year so far (table 1). This enthusiasm provides us with relevant data on the biology of owls.

Fidelity to the nest site and fidelity to the mate are life history characteristics which vary from species to species. In many studies on population ecology of a species (mortality studies, studies on life-time reproductive output etc.), knowledge about these strategies are of vital importance.

Although very little hard data have been published, it is more or less a dogma, that both the Ural Owl and the Tawny Owl are very faithful to their breeding sites, and that their pair-bond is life long (e.g. Mikkola 1983).

In this paper, I first describe the methods for capturing adults of these species at the nest and then discuss nest site and mate fidelity based on the Finnish ring recovery and retrap data.

Table 1.--Ringling of owls in Finland in 1986, and grand totals 1913-1986.

	1986 pullus	1986 full- grown	1913-1986 total
Eagle Owl			
<i>Bubo bubo</i>	719	4	4760
Snowy Owl			
<i>Nyctea scandiaca</i>	-	-	14
Hawk Owl			
<i>Surnia ulula</i>	140	16	1246
Pygmy Owl			
<i>Glauc. passerinum</i>	45	63	919
Tawny Owl			
<i>Strix aluco</i>	1201	143	19383
Ural Owl			
<i>Strix uralensis</i>	1569	120	12067
Great Grey Owl			
<i>Strix nebulosa</i>	9	1	796
Long-eared Owl			
<i>Asio otus</i>	530	162	6391
Short-eared Owl			
<i>Asio flammeus</i>	231	13	3386
Tengmalm's Owl			
<i>Aegol. funereus</i>	4044	1797	36120
Total	8488	2319	85016

MATERIAL AND METHODS

Capturing Adults at the Nest

If the nest is in a nest-box or similar natural cavity, the females can usually be captured very easily. If the opening of the box/cavity is covered by a capacious butterfly net, the female either tries to escape and jumps into the net, or stays in the nest, from which she can readily be taken by hand.

¹Paper presented at the Northern Forest Owl Symposium. [Winnipeg, Manitoba, Canada, February 3-7, 1987].

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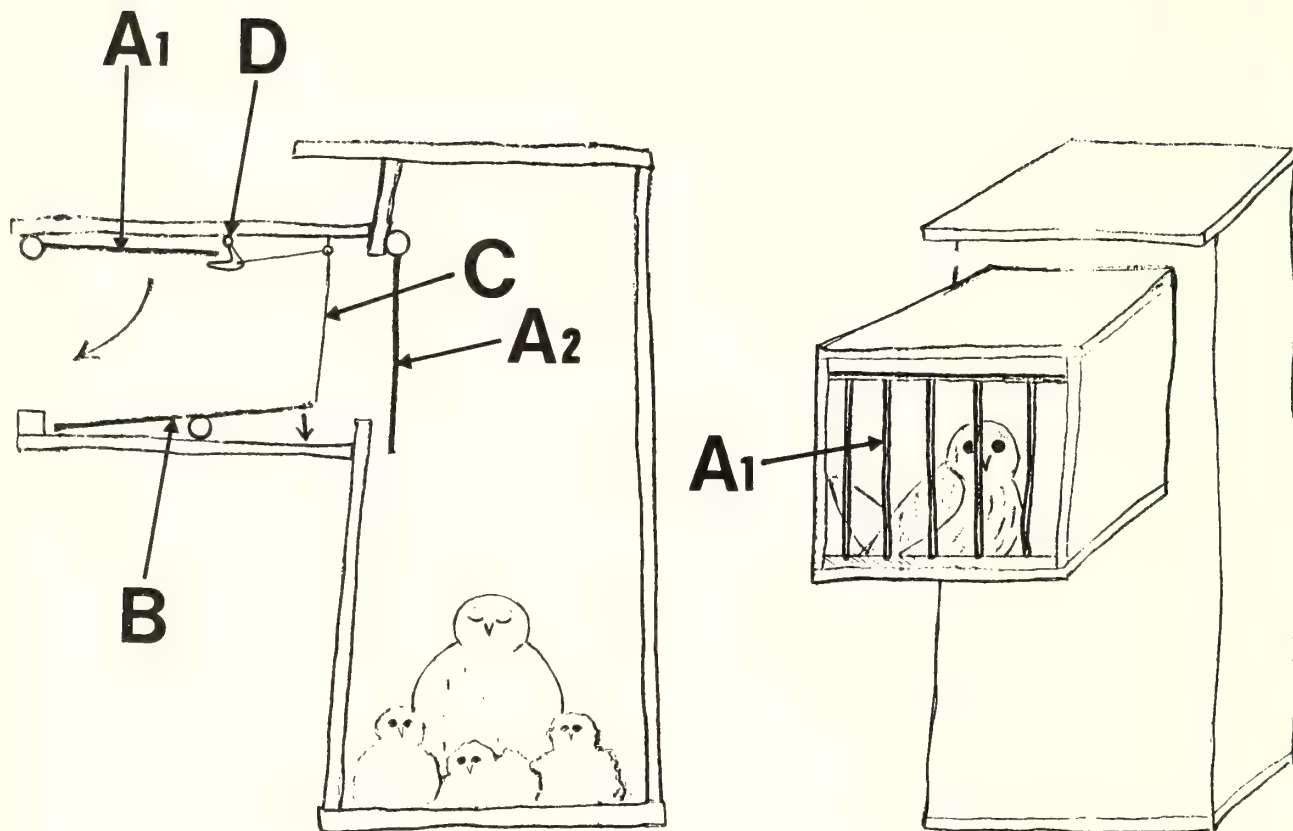


Figure 1.--A trap for capturing males. A1 and A2 are swing doors, made of vertical bars (horizontal bars cause injuries on the base of the bill), B is a swing board which is connected by a nylon line (C) to the releaser (D).

Ural Owls can safely be trapped during the whole period the female stays inside the nest-box, i.e. from the beginning of egg-laying through the first ten days of the nestling period. In contrast, Tawny Owl females should not be captured before the young are hatched, because this species is sensitive and is very likely to desert the nest if disturbed during the incubation.

Trapping of males is much more complicated and time consuming. I have used the following procedure. A couple of days after the young are hatched the female is shut in the nest-box and a trap for the male is attached to the front of the hole (fig. 1). In normal circumstances, the female answers, when the male hoots on returning with the prey. She flies out and receives the prey outside the nest-box. However, with the female shut in the nest-box, the male is forced to take the prey into the nest, and so enters, and is caught in the trap.

Almost all Tawny Owl males can readily be captured using this method. The Ural Owl

males are, in general, much more suspicious and some males are so difficult that more than one night (at 3-5 nights intervals) is needed to capture them. It is important that this extra disturbance is compensated for by giving extra food to the female and nestlings both before and after each trapping attempt.

Data Sets and Their Biases

Nest site fidelity is examined here on the basis of three kinds of data sets, which all are biased, but in different ways.

1) Data on owls captured at least in two breeding seasons at the nest in my study area ("Hauho", 61°10'N / 24°35'E, table 2). These data give reliable and comparable information, but only from a fairly small area: movements away from the study area can not be detected.

2) Data on owls captured during at least two breeding seasons at the nest over the whole of Finland (table 3). This data set gives more information on long distance

Table 2.--Maximum distances between two nest sites in sequence for each individual in the study area "Hauho".

Distance moved (km)	Number of birds			
	Ural male	Owl female	Tawny male	Owl female
0	47 (85%)	47 (60%)	21 (53%)	31 (61%)
1-5	8	28	18	18
6-10	-	3	1	-
11-15	-	-	-	2
Total	55	78	40	51

Table 3.--Maximum distances between two nest sites in sequence for each individual, total Finnish data. (Movements >30 km: Ural Owl female 160 km; Tawny Owl male 34 km, female 34, 40, 57, 58 and 68 km.)

Distance moved (km)	Number of birds			
	Ural male	Owl female	Tawny male	Owl female
0-5	55 (100%)	555 (96%)	109 (97%)	341 (90%)
6-10	-	17	2	15
11-20	-	3	-	15
21-30	-	-	-	3
>30	-	1	1	5
Total	55	576	112	379

movements, but because trapping-sites are patchily distributed and cover only a small part of Finland, the probability for a short distance retrap is higher than for a long distance one. Further, Ural Owl males have only been captured in my study area, and Tawny Owl males only in mine and two other study areas ("Valkeakoski", 61°15'N / 24°03'E by Pertti Nikkanen, and "Siuntio", 60°15'N / 24°15'E by Kimpri Bird Projects /Kari Ahola). Thus, only the females of both species have been caught extensively. Therefore this data is representative only for comparisons between the females.

3) Total Finnish data on owls captured at the nest and found dead at least 6 months later (table 4). The first weak point in this data set is, that if mortality among birds, which leave their territories because of a bad food situation, is higher than among those which stay, the probability for a long distance recovery is higher than for a short distance one. Further, because many of the Ural Owl nest sites are located in forests with a low level of human activities, the probability that a dead Ural Owl is found within it's territory may often be much lower than that it is found some kilometres away. The same

Table 4.--Distances moved by owls trapped at the nest and found dead >6 months later, total Finnish data. (Movements >30 km: Ural Owl female 97 and 219 km; Tawny Owl male 35, 37 and 57 km, female 34, 42, 45 and 89 km.)

Distance moved (km)	Number of birds			
	Ural male	Owl female	Tawny male	Owl female
0-5	10 (100%)	53 (85%)	28 (76%)	117 (76%)
6-10	-	3	3	17
11-20	-	2	1	10
21-30	-	2	2	6
>30	-	2	3	4
Total	10	62	37	154

problem does not emerge for the analysis of Tawny Owl recoveries, because this species is generally associated with areas of high human density throughout it's life.

RESULTS

Nest Site Fidelity

Fidelity to the breeding territory seems to be almost absolute in the Ural Owl male: so far all Ural Owl males have been encountered within a 5 km radius of the nest site used during the previous nesting attempt. However, the distance between two most remote nest sites of a Ural Owl male may be somewhat more than 5 km (see fig. 2). Ural Owl male differs significantly from the female and from both sexes of the Tawny Owl in nest site fidelity (table 2, comparison: no movement at all versus movement; $\chi^2 = 8.7$, $p < 0.01$).

For the Ural Owl female and the Tawny Owl, the estimate for fidelity to a nest site depends on the data set used. In a set of ordinary ringing recoveries (table 4), 85% of the Ural Owl females and 76% of both sexes of the Tawny Owl were reported from within 5 km from the last nest site, but the corresponding figures from the total retrap data (table 3) are 96%, (97%) and 90%. Both these sets of estimates are biased, in opposite directions (see Material and Methods).

According to all information from retraps, nest site fidelity of the female is significantly higher in the Ural Owl than in the Tawny Owl (table 3, comparison: movement < 5km versus movement >5km, $\chi^2 = 15.0$, $p < 0.001$), but the corresponding difference in ordinary ringing recoveries

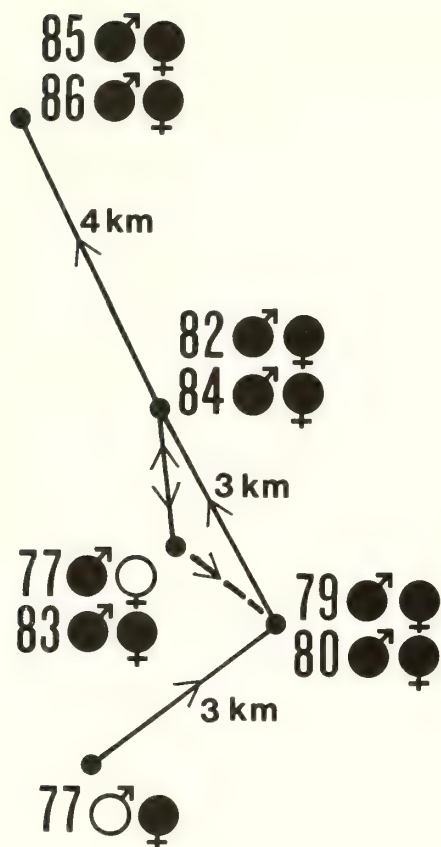


Figure 2.--Nest sites of a Ural Owl female and male (filled symbols) in 1977-1986.

is not significant (table 4; see Material and Methods for differences between the two species in recovery probabilities).

At the moment my best nest site fidelity estimates for the south Finnish populations are: 98-100% for the Ural Owl male, 90-95% for the female and 80-90% for the both sexes of the Tawny Owl.

Mate Fidelity

The example in fig. 3 shows clearly, that the pair-bond is not very strong in Finnish Tawny Owls. The average divorce rates (table 5) of 12% for the Tawny Owl and 3% for the Ural Owl must be understood as minimum values, because the probability of finding both members of a pair alive is very much higher, if they breed together at or near the previous nest site than if one (or both) has moved a longer distance.

My academic "guesstimates" for the real divorce rates are at the moment 15-20% for the Tawny Owl and 3-5% for the Ural Owl. None of the divorces in table 5 can,

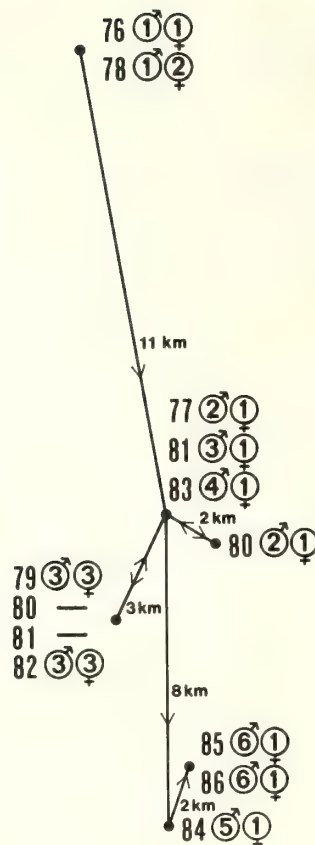


Figure 3.--Nest sites and mates of a Tawny Owl female in 1976-1986. The following divorces can be verified. 1) In 1977, female 1 moved away and paired with male 2; male 1 was found breeding with female 2 in 1978. 2) In 1981, female 1 paired with male 3, which left his territory and female 3. 3) In 1982, male 3 returned back to his previous territory and female 3; female 1 was found breeding in 1983 in the same nest box as in 1981.

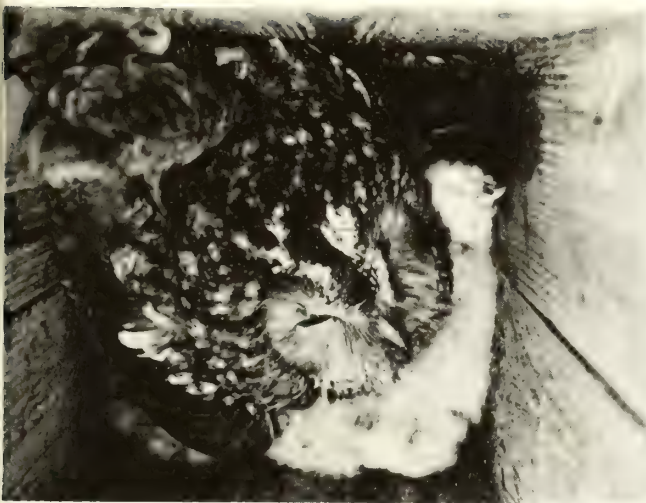
in my opinion, be attributed to unsuccessful breeding in the previous year.

In the 17 cases of divorce (table 5), male and female Tawny Owls have left their original territory and mate with almost the same frequency: in 10 cases only the female moved, in 6 cases only the male and in 1 case both.

DISCUSSION

Is There a Latitudinal Trend in Site Fidelity in the Tawny Owl?

In Tengmalm's Owl *Aegolius funereus*, a latitudinal trend from more nest site tenacious populations in Central Europe to



Tawny Owls in Finland.

Photos by Pekka Helo



site fidelity between Central European and Fennoscandian populations in this species, according to the data presented here.

In Tengmalm's Owl, the sexual differences in nest site fidelity have been seen primarily as a part of the reproductive tactics of the species: the females are more ready to change the breeding area than the males, which try to keep their nest hole, even in a cyclic environment, until the next favourable breeding season (Lundberg 1979). In the Tawny Owl, which is also a hole nesting species, no significant difference can be found in the nest site fidelity between the two sexes. For this reason, I suggest that the Tawny Owls, which have changed their territories, have moved primarily because of pressure to do with their winter survival rather than in search for a new and more favourable breeding area.

Why Is Nest Site Fidelity Stronger in Male than in Female Ural Owls?

The nest site fidelity of the Ural Owl has been postulated as being more or less absolute, partly on the basis of very scanty data and partly because of theoretical considerations (Lundberg 1979). The Ural Owl is a generalist feeder, which can survive even in severe winters, and breeds in suitable tree cavities, which are a scarce resource.

On the basis of my own data, there seems to be a relatively small but significant difference between the sexes. In the male the fidelity is absolute, but 5-10% (or even 15%) of the females leave their territories and can be found as much as 200 km or more away from their previous breed-

Table 5.--Divorce rates in the Tawny Owl and Ural Owl. N = number of cases, when both members of a pair were verified alive in a later breeding season, divorces= verified number of pairs separated. Hauho, Valkeakoski and Siuntio are study areas (see Material and Methods).

	N	divorces	divorce rate
Tawny Owl			
- Hauho	58	10	17.2
- Valkeakoski	42	1	2.3
- Siuntio	41	6	14.6
Total	141	17	12.1
Ural Owl			
- Hauho	113	3	2.7

the very nomadic ones in northern Fennoscandia has been described by Korpimäki et al. (1987). This trend in the reproductive tactics of the species has been attributed to the cyclicity in microtine populations which increases from south to north (see Hansson and Henttonen 1985).

Very little exact information, based on such techniques as radio-tracking or capture-recapture of breeding adults at the nest, has so far been published on the site fidelity of the Tawny Owl and Ural Owl. According to mostly indirect and scanty data available from Britain (Hirons 1985) and Central Europe (Delmée et al. 1978, Melde 1984), fidelity to the territory once selected seems to be almost absolute in both sexes of the Tawny Owl. Hence, there is presumably a real difference in the nest

ing site. This difference can be explained in three different ways.

1) As a general difference in the breeding strategy of the two sexes, described for many different groups of birds (e.g. Greenwood and Harvey 1982) and including different responses to the death of the mate: the female can begin to search for a new mate and territory, but the male must guard his nest hole and wait for a new mate.

2) As an indication of higher readiness for nomadism (change of breeding area according to the food situation) in the female than in the male as was found in Tengmalm's Owl (Korpimäki et al 1987, see above).

3) As a consequence of the female's reduced ability, as the less skillful hunter of the two sexes, to survive a really hard winter famine.

At the moment none of the alternatives can be preferred on the basis of hard data. One very recent ring recovery (not included in table 4) suggests that at least some females have probably moved only because of famine: a female, which bred successfully for 10 years in the same territory, was found dying 70 km from her nest site in January 1987 during an exceptionally cold period after a crash of vole populations.

Does a Real Pair-Bond Exist in the Ural Owl and Tawny Owl?

In the literature (e.g. Mikkola 1983) both the Tawny Owl and Ural Owl are listed, without presenting any hard data, with the species whose pair-bond is life-long. Present data from Southern Finland indicates that annually at least 15-20% (or even more) of Tawny Owl pairs separate, but only 3-5% of the Ural Owls.

In some species, e.g. in the Kittiwake (Coulson and Thomas 1983) failure during the previous breeding season is probably the most important cause for divorce. On the other hand, Newton and Marquiss (1982) concluded, that the food situation is the only decisive factor for mate fidelity in the Sparrowhawk. This conclusion is probably valid also for the Tawny Owl and Ural Owl.

Is there any "real" pair-bond in the Tawny Owl and Ural Owl? Do members of a pair breed together, with the observed probability, only as a consequence of their relatively high nest site fidelity? For a reliable answer much more detailed information, including radio-tracking of several individuals is needed. At the moment I am ready to suggest, that the pair-bond in the Tawny Owl can be explained merely as fide-

lity of the both sexes to the nest site and breeding territory. In contrast, some of the Ural Owl pairs have moved together to new nest sites over such long distances (fig. 2), that any explanation which does not accept the existence of a real pair-bond in this species is difficult.

Acknowledgements. Kari Ahola (Kimpäri Bird Projects) and Pertti Nikkanen put their original data at my disposal. Mika Kilpi and Chris Mead made valuable comments on the first draft of the manuscript. Jukka Haapala and Kirsi Hutri draw the figures.

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Nest Platforms for Great Gray Owls¹

Evelyn L. Bull,² Mark G. Henjum,³
and Ralph G. Anderson⁴

Abstract.--During 1983-1986, 12 great gray owl (*Strix nebulosa*) pairs nested on artificial platforms in northeastern Oregon. Platforms put up 15 m were preferred over those platforms put up 9 m. Nest platforms were preferred over nest boxes. Each platform cost \$40 to construct and mount.

The loss of natural nest sites has encouraged use of artificial nest structures for owls (*Strix* spp.) in northern Europe (Stefansson 1978, Rauhala 1980, Hilden and Helo 1981, Mikkola 1983, Helo 1984), and Canada (Nero 1980). In the Pacific Northwest, great gray owls (*S. nebulosa*) frequently nest in vacated hawk nests or on the broken tops of dead trees. Intensified timber management has reduced the number of available nest sites because many large diameter dead and live trees have been harvested.

At least 5 types of nest structures have been constructed for and used by great gray owls. Helo (1984) described an open nest structure 40 x 30 cm with a height of 10 cm that great gray owls have used. Nest structures used in Canada and Minnesota include wire frames with sticks inside (Nero et al. 1974, Nero 1982), wire baskets with sticks inside (Bohm 1985), and nests constructed of sticks alone (R. W. Nero, pers. comm.). Quinton (1984) described nests created by cutting the tops off trees and making a shallow depression inside the bole.

Great gray owls readily use artificial structures (fig. 1); we wanted to determine if the owls had a preference for height of nest (placed at 9 m or 15 m above the ground), type of nest (wooden platforms or nest boxes), and

distance of nest from a clearcut (adjacent to a clearcut or 100 to 200 m from the edge of a clearcut).

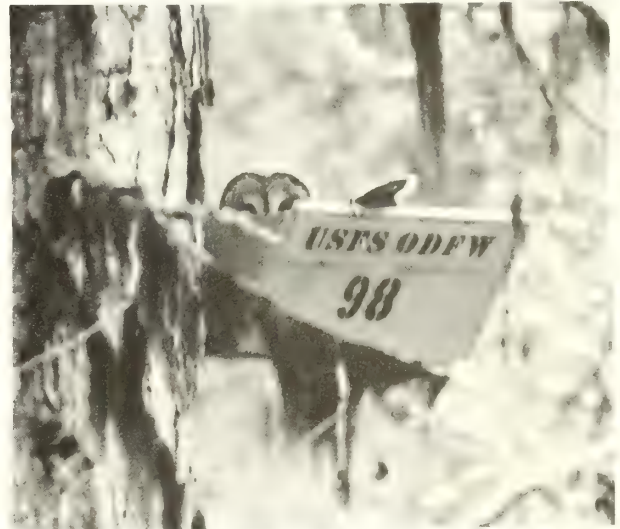


Figure 1. Female great gray owl nesting on wooden platform in northeastern Oregon, 1986.

METHODS

We established 3 study areas in the Blue and Willowa Mountains in northeastern Oregon where mixed conifer forests were interspersed with openings. In study area A, we selected 26 sites and put 2 platforms (fig. 2) at each site, in separate trees but within 30 m of each other. One platform was 9 m and the other was 15 m above the ground.

In study area B, we selected 27 sites near clearcuts created 1 to 10 years ago. At each site, 1 platform was adjacent to the clearcut

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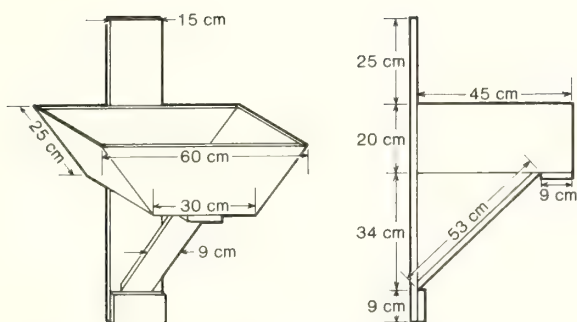


Figure 2.--Great gray owl nest platform constructed from 2-cm thick boards. Holes were drilled for 20-cm long ring-shank nails used with washers. Platforms were stained with 5 parts linseed oil and 1 part gray stain.

and 1 in a forest stand 100 to 200 m from the edge of the clearcut. Platforms were put 9 m above the ground.

In study area C, we selected 26 sites and put 1 wooden platform and 1 wooden nest box (fig. 3) at each site. Each platform was within 30 m of a box, and both were 9 m above the ground. An additional 28 wooden platforms were erected in study area C between 1975 and 1985 but were not part of this study. The platforms, 9 m above the ground in forested stands, were checked irregularly over the years.

Sites were at least 0.5 km apart--the minimum distance we found between active nests of great gray owls. Sites for platforms were selected based on historic use by great gray owls and the presence of mature trees.

Platforms were placed on the northeastern side of live trees _ 30 cm dbh (diameter at breast height) to reduce solar heat. Branches were removed along the bole from the ground to 1 m above the platform to allow access by the birds. An 8-cm layer of chips was placed in the bottom of platforms and boxes with twigs 1 cm in diameter placed on top. This chip layer permitted birds to dig depressions in which to lay eggs. Holes (1 cm in diameter) were drilled in the bottom of platforms and boxes for drainage.

The nest structures were put up in September 1984 in study areas A and B, and in summer 1982 in study area C. Each structure was checked annually in late April because great gray owls usually started incubating in late March. The female's tail was usually visible over the edge of the nest structure.

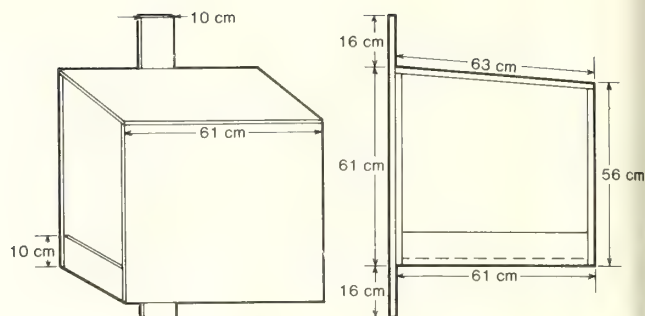


Figure 3.--Great gray owl nest box constructed of 1-cm thick plywood. The vertical support piece was a 2 x 10 cm board. Holes were drilled for 20-cm long ring-shank nails used with washers. Platforms were stained with 5 parts linseed oil and 1 part brown stain.

The cost of constructing and mounting the platforms was calculated using \$5 for materials/platform, \$7/hr for labor, and \$0.10/km for vehicular travel. Eight platforms could be erected in a 10-hr day. To construct and mount, each platform cost \$40.

RESULTS

From 1983 to 1986, 12 great gray owl pairs nested on these platforms (table 1). All 5 pairs that nested on platforms in study area A used the platforms 15 m above the ground. Two pairs nested in study area B, 1 on a platform adjacent to a clearcut and 1 on a platform 200 m from a clearcut. All 5 pairs that nested in study area C used wooden platforms. None used nest boxes. Ten of the 12 nesting pairs successfully fledged young. At least 5 of the additional 28 platforms in study area C were used by nesting great gray owls during 1980-1986.

Great horned owls (*Bubo virginianus*) nested on 1 platform in 1985 and on 5 platforms in 1986.

DISCUSSION

Great gray owls preferred the wooden platforms to the boxes and preferred the 15-m to the 9-m height, although the 9-m height was used when other suitable platforms were not available (as in study areas B and C). Platforms adjacent to and 200 m from a clearcut were used. Great gray owls sometimes used wooden platforms when natural nest sites were available nearby.

Table 1.--Number of artificial platforms used by great gray owls for nesting in northeastern Oregon, 1983-1986.

Study area	Year			
	1983	1984	1985	1985
A-Nest height (26 sites)				
9 m	NA ¹	NA	0	0
15 m	NA	NA	2	3
B-Proximity to clearcut (27 sites)				
Adjacent	NA	NA	0	1
100-200 m away	NA	NA	0	1
C-Nest structure type (27 sites)				
Platform	1	1	1	2
Box	0	0	0	0

¹ Platforms not put up until September 1984.

The number of pairs that fledged young was higher for those pairs that nested on wooden platforms (83%) than for pairs that nested on stick nests, mistletoe clumps, or broken-topped dead trees (70%) (unpublished data, E. L. Bull). This higher success was partly because the platforms are stable; eggs or nestlings sometimes fell through stick and mistletoe nests.

A potential problem exists with great horned owls using the platforms because great horned owls are a major predator of fledged great gray owls (Nero 1980). We did not anticipate this problem because the great horned owl nests we had observed before 1984 were in more concealed sites than the ones we offered. Because great horned owls nest 1 to 3 weeks earlier and are more aggressive, they could successfully compete with great gray owls for nest sites on platforms. The subsequent increase in great horned owls could take its toll on fledged great gray owls in the area.

Mikkola (1982, 1983) addressed a similar problem installing artificial nest structures for the tawny (*S. aluco*) and ural owls (*S. uralensis*) in Europe. The tawny and ural owls prey on smaller owls, and in areas where artificial nest structures were used by tawny or ural owls, the smaller owls disappeared (Schonn 1980).

Thus, nest platforms can provide nest sites for great gray owls, but caution is needed because platforms could also increase populations of great horned owls, which could be detrimental to great gray owls. Given the rarity of great gray owls and the attraction the species has to segments of the public, the cost of providing artificial nest platforms is justified.

ACKNOWLEDGMENTS

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Biology of the Great Gray Owl in Interior Alaska¹

Timothy O. Osborne²

Abstract.--The great gray owl was found frequently in the Yukon and Koyukuk River lowlands from 1981 to 1984 in successional white spruce forest. The owls occupied winter roosts which were habitually used in successive years. Yellow-cheeked vole (*Microtus xanthognathus*) composed 66%, by frequency, of the diet, other microtines composed 28%, and other mammalian and avian prey composed 6%.

INTRODUCTION

The status of the great gray owl (*Strix nebulosa*) in Alaska is thought to be scarce or rare (Armstrong 1980); however, Gabrielson and Lincoln (1957) said the bird was found regularly but was by no means common. Brandt (1943) said it was "common in the heavily wooded bottomlands" and Dall and Bannister (1869) took eight specimens 20 miles east of Nulato in 1867-1868. Studies in Manitoba (Nero et al. 1984), Saskatchewan (Harris 1984), Idaho (A. Franklin pers. commun.) and Alaska (present study) have found that the bird can be found with predictable regularity once the habitat requirements are defined. In Alaska, from at least 1981 to 1984, the great gray owl was at a population peak which contributed to my ease in finding the birds. These "population highs" have been previously noted in Europe (Mikkola 1973) and Manitoba (Nero et al. 1984). It is of interest that the 1981-1984 population high I recorded appeared to also occur in the Manitoba-Minnesota region (R. Nero pers. commun.).

STUDY AREA AND METHODS

My study was conducted in the floodplain areas adjacent to the confluence of the Yukon and Koyukuk Rivers. The majority of the data was collected from an 82 km² area located 5 km east of Bishop Rock (64°49'N, 157°22'W), on the islands and north bank of the Yukon River (fig. 1). Bishop Rock is located 24 km downriver from Galena and 35 km northeast of Nulato. The floodplain, varying from 10 to 25 km wide, is the product of extensive meanders of the Yukon

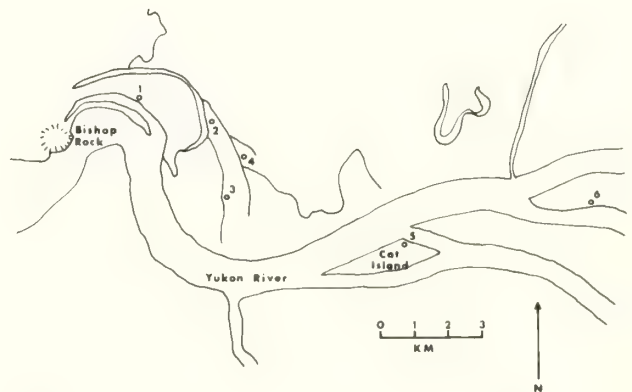


Figure 1.--Bishop Rock study area. Location of great gray owl nests (o) in 1984.

River over thousands of years. Away from the main channel are old levees with varying stages of succession ranging from willow (*Salix* spp. dominated communities through balsam poplar (*Populus balsamifera*) stands to white spruce (*Picea glauca*) dominated communities. Adjacent to the old levees are oxbow lakes also in varying stages of succession from open water through reed grass (*Calamagrostis* sp.) meadows to willow/alder (*Salix* sp./*Alnus* sp.) meadows. In some areas these levees and oxbow remnants form concentric habitat bands. Interspersed are blocks of land with extensive permafrost layers close to the surface which only support an open community of stunted larch (*Larix laricina*), black spruce (*Picea mariana*), and bog-associated shrubs.

Climate in the area is continental subarctic characterized by great seasonal extremes of temperature ranging from -55°C to 33°C and daylight ranging from 3.5 h to 21.5 h. Ice is present from early October to late May, and average yearly snowfall is about 137 cm (Selkregg 1976). Flooding of low-lying areas is infrequent and can be caused by two different events: ice

¹Paper presented at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

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jam floods or high-water floods. During winter 1984-1985, deep snow up to 2 m in the Yukon and Tanana River drainages produced a high-water flood which inundated many of the old oxbow areas for up to three weeks.

Data on the owls were collected opportunistically during studies of moose (*Alces alces*). Observations were conducted at irregular intervals from January 1982 to February 1987; however, most data were collected during winter and spring months. Nest trees were climbed, if possible, and contents recorded. At nest sites, prey remains and pellets were collected. At winter roosts, pellets were collected monthly by digging through the snow and after snowmelt in June. At one site a 1.5 x 1.5 m pellet collector was constructed using a 2 x 4 wooden frame covered with plastic sheeting forming a funnel. A plastic bucket with water drain holes was placed below the funnel throat to catch the pellets. The pellet collection device was abandoned after black bears (*Ursus americanus*) ate the plastic components. Pellets were dissected, and I identified prey remains by skull and tooth characters using voucher specimens from the University of Alaska Museum.

Three small mammal traplines were run along the Yukon River during late August 1984 and 1985 to ascertain relative prey densities. Each trapline had 20 stations 17 m apart, with two Museum Special snap traps baited with peanut butter and one pitfall funnel trap at each station. Each line was run for three consecutive nights. One line was in a permafrost bog/open black spruce community running perpendicular to the river, one line was in a mature balsam poplar stand running parallel to the river and the third site was 1 km from the river in a (*Calamagrostis* sp.) meadow. In 1985 the meadow site was covered with 0.5 m of water for 19 days during June, prior to trapping.

During intensive aerial moose surveys, I occasionally observed great gray owls either perched on meadow edges or as they flushed from tree roosts. The surveys were conducted using a Super Cub aircraft flying at 112 kmph at 100 m above ground level with a minimum ground search intensity of 4 min/mi². The observations produced a relative index of abundance which was biased due to varying sightability of the owls and their individual reactions to aircraft (some would flush and some would not). Sixteen surveys were flown in November and one in April. Data were used from the following moose trend areas: Kaiyuh Slough near Nulato; Squirrel Creek near Koyukuk; Three Day Slough (65°29'N, 157°30'W); Deep Creek 20 km NW Ruby; and Nowitna/Sulatna Rivers confluence (64°36'N, 154°28'W). Another method used to determine density was vocalizations by the owls, either during certain daylight periods or at night. I usually would initiate calling by imitating the owl's call and then listening for responses and calculating their positions.

RESULTS

The great gray owl occurred in successional white spruce lowland forests along the Yukon River. The meadows of grasses and sedges provided habitat for voles (*Microtus* spp.), were open hunting areas, and were fringed with willows and balsam poplars which provided hunting perches. Decadent balsam poplar and white spruce provided nesting sites. The area also had large breeding populations of common raven (*Corvus corax*) and red-tailed hawks (*Buteo jamaicensis*), which provided potential nest platforms. Mature spruce stands provided sheltered winter roost sites.

During the winter months, October to March, owls were found during daylight periods perched on the edge of open areas, such as meadows, creeks, sloughs, or along the main rivers. During the breeding season, April to July, the owls were always perched at or near the nest site. I was unable to observe owls while they were hunting during this period. I rarely observed owls once fledging occurred until winter conditions allowed access to the areas away from the river.

I was unable to ascertain if the owls were residents in the area or migrants, but since my sightings were mainly in the winter months, I suspect the birds were residents. I do not believe the breeding population was augmented by birds from other areas.

Nesting

The study area had no man-made nesting structures, thus the density of owls was dependent upon natural regulatory factors. Great gray owls do not build nests and are limited to available nest sites (Nero 1982). If there are sufficient nest sites, then other factors, such as food supply, regulate the population. Along the Yukon River, I found raven nests approximately every 1.5 km and decayed balsam poplar stumps, similar to those used for nesting, occurred very frequently. I found six owl nests in the 82 km² study area during 1984. The nests averaged 2.8 km apart (range 0.6 to 5.2 km). The density of breeding owls I found (fig. 1) was probably a minimum since it was impossible to search the entire Bishop Rock area. During nocturnal owl calling sessions, at least two more owls were calling adjacent to the area to the north. Owls, presumably breeding, were also seen on the south bank of the Yukon River. In the Three Day Slough area, during an overcast day in late March 1984, six different owls were calling in a 78 km² area. Mikkola (1981) noted that in Finland, calling during the day had never been reported.

I found a great gray owl nest on 5 June 1983 when it held two 300-400 g chicks. It was in an old raven nest near an area where I had seen owls in spring 1982. In March the nest had owl feathers and pellets on top of the snow-covered structure. On 24 June the nest was empty and the young were gone.

In 1984 I located 15 old raven nests in the area between Bishop Rock and Galena. The 1983 nest had signs of visitation, since the snow was "tramped" down, but no owls were seen at the nest by 14 April. On 15 April, I flushed a female great gray owl from a 4 m high balsam poplar stump (fig. 1, no. 3). She immediately returned to the stump and behaved as though she was incubating eggs. A male was perched nearby. On 19 April I checked all the old raven nests and likely stumps everywhere I had previously seen owls perched. I found five more occupied great gray owl nests. Three were in old raven nests (fig. 1, nos. 1, 5, 6), one was in a balsam poplar stump (fig. 1, no. 3), and one was in a white spruce stump (fig. 1, no. 4). Five of the nests were in balsam poplar woodland and one nest was in a white spruce-birch (*Betula* spp.) woodland. Only three of the nests were in trees I was able to climb. By 28 April two nests had a clutch of four and one had a clutch of five eggs. Four pairs produced three young each and two nesting attempts failed. I think two of the 1984 nest sites (nos. 3, 4) were active during the 1983 nesting season based on old pellets found under the leaf litter in 1984.

In 1985 owls were rarely seen during the winter. I checked all the previous nests and no eggs had been laid by the end of March. I checked the six old nests on 27 May and found two with incubating females (nos. 1, 3). One nest had two eggs on 5 June. On 22 June this nest had one dead 77 g chick and one live 150 g chick. The dead chick had an empty stomach and no fat reserves, which indicated that it died of starvation. On 5 July both nests had one young each. The very late laying dates, compared with 1984, may have been caused by the deep snow conditions. A. Franklin (pers. commun.) noted a three-week delay in mean egg-laying dates in Idaho following deep winter snow conditions.

In 1986 the nest sites were checked once in early May and none of the nests were active.

Roosts

In May 1982 I found a collection of owl pellets on the ground below a white spruce tree. There were numerous feathers of great gray owls scattered around and in the branches of the tree. Some of the pellets were on top of dried leaves, having been deposited during the previous winter; others were under the leaves and buried in the moss, indicating that they were deposited during or prior to leaf-drop in 1981. The roost was located on a levee area in a dense stand of white spruce, but only 20 m from an open slough. Although I never observed an owl at the roost, I suspect that the roost was used at night and during periods of cold weather, but verification was not possible since the roost could not be approached undetected and it was not safe to travel during weather colder than -40°C. The bird or birds mainly used the one tree, but some alternate roost trees were found. The main roost was in use each winter up to December 1984, at

which time it was abandoned. I did not check on the roost during winter 1985-1986, but the roost was in use again during December 1986. In other areas, more groups of pellets below spruce trees were found, indicating other habitual roosts. Habitual winter roosts have not been previously recorded for the species (*R. Nero* pers. commun., Mikkola 1981).

Diet

The information on diet of the great gray owl in Alaska is scant. They are said to eat "mice and other small mammals and birds" (Gabrielson and Lincoln 1957) and "mice and ground squirrels" (Armstrong 1980). In my study area, of 411 prey items, microtine rodents composed 94% (table 1). Other mammals and birds composed only 6% of the diet. Pellets (n=99) were collected from one nest in 1983, five nests in 1984, and two nests in 1985. At nest sites voles were the main prey items, but species composition was different at winter roosts (table 1). Yellow-cheeked voles (*Microtus xanthognathus*) was the most important prey item (76.8%) during the winter months, but dropped to half (48.1%) during summer. Results of a χ^2 test of these differences in seasonal preference are significant at the 0.01 level. The average number of microtines per pellet (n=114) was greater during winter (2.13 individuals/pellet) than during summer (1.28 individuals/pellet). The smaller number of individuals during summer may have been due partially to pellets from nestling birds being included in the sample.

The slight increase in the number of birds (table 1) in summer is probably due to the greater number of birds present in the habitat compared with winter.

DISCUSSION

The reference by Armstrong (1980) to great gray owls eating ground squirrels (*Citellus parryii*) is probably an error and his source cannot be found (*R. Armstrong* pers. commun.).

Table 1.--Great gray owl prey analysis from winter roosts and nests, Yukon River, Alaska, 1982-1985.

Species	Winter roosts		Nests	
	number		number	%
Mammals				
<i>Microtus xanthognathus</i>	196	76.8	75	48.1
<i>Microtus pennsylvanicus</i>	22	8.6	52	33.3
<i>Microtus oeconomus</i>	4	1.6	2	1.3
<i>Microtus</i> spp.	--	--	4	2.6
<i>Clethrionomys rutilus</i>	23	9.0	8	5.2
<i>Syaptomys borealis</i>	4	1.6	3	1.9
<i>Sorex</i> spp.	1	0.4	--	--
<i>Mustela erminea</i>	1	0.4	--	--
<i>Lepus americanus</i>	--	--	1	0.6
Birds				
Grouse	2	0.8	1	0.6
<i>Perisoreus canadensis</i>	--	--	1	0.6
Passerine bird	--	--	1	0.6
Unidentified feathers	2	0.8	8	5.2
Totals	255	100.0	156	99.9

The habitat of the ground squirrel (dry tundra) and the owl do not overlap. I never recorded the abundant and much more likely red squirrel (*Tamiasciurus hudsonicus*) in the owl's diet.

At nest sites, the meadow vole (*Microtus pennsylvanicus*) was only recorded in 1984 and 1985 which suggests that either meadow vole populations were low or the feeding area of the 1983 nest was not occupied by the vole. I suspect the vole population may have been low. At the roost, meadow voles composed only 4% of 124 microtines caught during 1982 and 1983, but 13% of 115 voles during 1984.

The results from the small mammal trapline indicated that the great gray owl was a selective predator. Shrews were abundant in the area in all habitats (table 2), composing 39% of the total animals caught, yet only one individual was found in the pellets (table 1). Mikkola (1981) compared the fall and winter diet of owls from Finland, Sweden, Canada, and USA and found the frequency of insectivores was 48.7, 21.5, 23.5, and 12.5%, respectively. However, in Finland the winter prey items may have been biased because they were from stomach contents of road-killed owls during years of low vole populations.

All great gray owl nests in California have been in broken off stumps (A. Franklin pers. commun.), in southern Oregon they used old goshawk (*Accipiter gentilis*) nests³, in Idaho they utilized a 58:42 ratio of stumps and old raptor nests (A. Franklin pers. commun.), and in Canada all the nests were in old raptor nests or man-made raptor-like nests (Nero 1980). All previous owl nests in Alaska had been found in old raptor nests, almost all in old goshawk nests (D. G. Roseneau pers. commun.; Alaska Department of Fish and Game raptor records; Gabrielson and Lincoln 1957). There appeared to be a clinal behavior of the owls tending toward old raptor nests in the north and stumps in the south. The introduction of man-made nest platforms clouds the trend. Mikkola (1981) found a similar cline in Finland. He found the owl nesting more frequently in stumps in the south and almost all the nests in the north were in old goshawk nests. The reasons for the tendency to use raptor nests in the north may be related to the decrease in tree size and circumference in northern latitudes. Logging practices and frequent fires in Canada may reduce the number of suitable stumps.

I concentrated my efforts in searching for old hawk and raven nests. Goshawks were occasionally seen in the study area, but for nesting they prefer hillsides with aspen (*Populus tremuloides*) or paper birch (*Betula papyrifera*). Seven red-tailed hawk nests were located in the area

³Forsman, E. D. and T. Bryan. 1984. Distribution, abundance and habitat of Great Gray Owls in southcentral Oregon. Rep. to Dep. Fish and Wildlife, Bend, Oregon, 30 June 1984.

Table 2.--Numbers of small mammals caught in three habitats during August, 1984 and 1985, Yukon River Alaska. Results from 90 trap-nights/habitat/year.

Species	Open black spruce		Balsam poplar		Grass meadow	
	1984	1985	1984	1985	1984	1985
<i>Microtus xanthognathus</i>	0	0	0	2	11	0
<i>Microtus pennsylvanicus</i>	0	1	0	0	1	19
<i>Clethrionomys rutilus</i>	7	21	35	33	3	0
<i>Syaptomys borealis</i>	0	0	0	0	1	0
<i>Sorex cinereus</i>	20	4	24	1	20	4
<i>Sorex hoyi</i>	0	2	0	1	0	1
<i>Sorex tundrensis</i>	0	0	1	2	0	0
<i>Sorex</i> , spp.	2	0	3	1	0	1
Totals	29	28	63	40	36	25

and none were used by the owls for nesting. Perhaps the reason red-tailed hawk nests were not used may be because they build their nests closer to the top of the canopy. Thus their nests may expose the owls to harassment of passing raptors, or the young may be more subject to heat stress from the sun. All the nests selected by great gray owls were within the canopy of the tree or stand. Both ravens and goshawks build their nests below the canopy, usually at a level which is 2/3 the height of the tree. Of the nine nesting attempts, the owls used old raven nests five times and stumps four times. The use of stumps for nest sites in Alaska has not previously been recorded.

I believe that the owl population was high from the beginning of my study, although the breeding data I collected may indicate that the owl population increased from 1981 to a peak in 1984. The apparent increase was due to my increased familiarity which enabled me to find more pairs. The owl population in Alaska has probably undergone fluctuations in the past. This would account for the discrepancies in its status as reported earlier (Dall and Bannister 1869, Brandt 1943, Gabrielson and Lincoln 1957). The exact location where Dall (Dall and Bannister 1869) collected his owls is unknown. He reported the site as Takatisky, 20 miles east of Nulato. The location of Takatisky is attributed to the Kaiyuh Hills (Orth 1971); however, Zagoskin (Michael 1967) used the name "Takayaska" for both the Kaiyuh Hills and a settlement at the confluence of the Yukon and Koyukuk Rivers. If the location was 20 miles due east of Nulato, as reported by Dall, then the Bishop Rock study area is only 5 km north of where Dall collected his data.

I observed a decline in the breeding population of the owls over the period 1984-1986. The relative abundance of the owls observed

Table 3.--Aerial sightings of great gray owls during moose surveys, Middle Yukon River area, Alaska.

Year	1982	1983	1984	1985	1986
Owls observed	9	3	4	1	0
km ² surveyed	799	543	606	484	216
Relative density birds/km ²	1/89	1/181	1/151	1/484	0/216

during winter moose surveys also declined from 1984 to 1986 (table 3). I attributed the decline to the abnormally deep snow during winter 1984-1985 and a consequent reduction in food supplies (voles) following the 1985 flood of the meadows. After the flood, the vole species composition of the grass meadow changed from yellow-cheeked vole (*Microtus xanthognathus*) to meadow vole (*M. pennsylvanicus*) and the total numbers were reduced (table 2). Yellow-cheeked voles are dominant over other *Microtus* species in Alaska, and their presence in an area would tend to lower populations of the other voles (Wolff and Lidicker 1980). Presumably after the flood, meadow voles were able to recolonize the meadow faster than yellow-cheeked voles. Yellow-cheeked voles are very active diurnal voles and are the largest vole in Alaska, with males averaging 120 g (Wolff and Lidicker 1980). Deep snow during winter could have impaired owl hunting efficiency which caused them to emigrate from the area, winter roosts were abandoned, and owl hunting plunge-marks in the snow were only infrequently observed.

The presence of great gray owl hunting plunge-marks (see Nero 1980 for photographs) could be used as an indicator of owl habitat use, prey densities, and owl densities. As a method, its advantage is that owls do not have to be directly observed to detect their activities. I realized the value of using plunge-marks to indicate owl habitat use and density during December 1984. The snow was falling frequently and deep enough to make plunge counts a useful method; however, when I visited the area in January 1985 no owls were using the area and thus the method remains untested here.

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A Floristic Analysis of Great Gray Owl Habitat in Aitkin County, Minnesota¹

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Abstract -- The floristic community associated with fourteen Great Gray Owl (*Strix nebulosa*) nest sites (Loch, in lit.) was analyzed. The overstory was dominated by black ash (*Fraxinus nigra*) and basswood (*Tilia americana*) and the prevalent shrub layer species included currants (*Ribes* sp.) and silky dogwood (*Cornus amomum*). Ginger (*Asarum canadense*), bedstraw (*Galium* sp.), wild strawberry (*Fragaria virginiana*), and jewelweed (*Impatiens capensis*) were common in the ground layer. Most of the nest sites were of the *Cornus Carex* sp.-*Caltha palustris* habitat type according to Mueller-Dombois (1974). Conversion of this habitat type for farming or mining poses a long-term threat to Great Gray Owl habitat in Aitkin County.

INTRODUCTION

The objective of this study was to describe the nest site habitat of the Great Gray Owl in Aitkin County, Minnesota. The effects of land use practices on the owl's habitat will be discussed.

SITE DESCRIPTION AND METHODS

Site Description

The Aitkin County study area, approximately 20 square miles in area, is located in north central Minnesota. Elevations within the study area range from 1235-1266 feet above sea level. The January mean temperature is approximately 4 F., the July mean temperature is about 66 F., and the mean annual precipitation is approximately 26 inches (Clapp, 1981).

The area is a mix of tamarack-black spruce (~50%), open communities composed of grass and sedge meadows or other open situations (~30%), and hardwood communities (~20%). The soils are predominantly organic in nature.

METHODS

A 400 square meter plot, 20 meters on a side, was centered on each nest tree. The plot size is a modification of the recommended tenth-acre circular plots (James and Shugart, 1970; Titus and Mosher, 1981). All trees over five meters in height (Mueller-Dombois and Ellenberg, 1974) were measured for diameter at breast height with a diameter tape and for height with a Spiegel-Relaskop. Each tree was rated as to its position in the canopy (Smith, 1962). The nest tree and three other dominant or codominant trees were drilled with an increment borer to determine age. At four locations in the plot, per cent cover was determined using a densiometer.

For this study the shrub layer was defined as plants, generally woody perennials, ranging in height from 50 centimeters to 5 meters (Mueller-Dombois and Ellenberg, 1974). The average height, cover (Daubenmire, 1968), and dispersion (Braun-Blanquet, 1965) will be recorded for each shrub species within the 400 square meter plot. The plot was transected four times in order to describe the understory.

The ground layer was defined as plants, usually herbaceous, that are less than 50 centimeters in height (Mueller-Dombois and Ellenberg, 1974). Two smaller plots, measuring 2 meters by 1 meter and located in a regularized pattern within the larger plot, were used to study the herbaceous layer. Each species' cover and dispersion were ocularly estimated using the same scales applied to the shrub layer.

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In addition to conventional soil information, a soil scientist from the U.S. Soil Survey visited some of the nest sites and contributed to the habitat analysis. Plant and soil data were combined to classify the habitat in accordance with a "Key for Mapping Forest Habitat Types in Southeast Manitoba. . . ." (Mueller-Dombois, 1974).

RESULTS

Nest tree and site data are summarized in table 1. All but two of the nest trees, whose tops had recently been damaged, were in dominant positions in the canopy. Twelve of the fourteen nest trees were hardwood species. Also, all except one nest tree was taller than the average height for the plot. Nine sites had less than 10% cover, twelve sites had less than 30% cover and all fourteen sites had less than 45% cover.

The nest sites as well as the nest trees were dominated by hardwood species especially black ash (*Fraxinus nigra*) basswood (*Tilia americana*), american elm (*Ulmus americana*), red maple (*Acer rubrum*), and sugar maple (*Acer saccharum*) (see table 2). In the shrub layer black ash, *Ribes* sp., hazel (*Corylus cornuta*), silky dogwood (*Cornus amomum*), and american elm were the most common species (see table 3). Ginger (*Asarum canadense*), bedstraw (*Galium* sp.), wild strawberry (*Fragaria virginiana*), canada mayflower (*Maianthemum canadense*), sarsaparilla (*Aralia nudicaulis*), violets (*Viola* sp.), jewelweed (*Impatiens capensis*), and species of sedge (*Carex* sp.) were the most common species in the ground layer (see table 4).

According to material supplied by the Soil Conservation Service, over three quarters of the soils in the twenty square

mile study were formed in organic materials. Twelve of the fourteen nest sites, however, were on soils formed in glacial till. These mineral soil series (see table 1) are generally poorly drained fine sandy loams that are either thinly covered by or include pockets of organic soil. Eight of the twelve mineral soil sites are Alstad loam. The two nest sites on organic soils are both Cathro muck. Standing water can be found on almost all the soils in the study area particularly after rains and during spring run-off.

Not surprisingly, the Mueller-Dombois (1974) key to forest habitat types characterize all of the nest sites as "Habitats with excessive soil moisture." Twelve sites are a flood water association described as the *Cornus-Carex* sp.-*Caltha palustris* type (ew). *Fraxinus* sp. and *Larix laricina* are often found growing in the ew type (see table 1). The other two sites are on a bog type described as the *Betula pumila-Carex-Caltha-Potentilla* type (BC). *Larix laricina* is the most common tree found growing in this habitat.

DISCUSSION

Great Gray Owls do not construct or maintain the nests they occupy (Nero, 1980) and, as mentioned earlier, much of their habitat is dominated by a tamarack swamp system. The small size and pyramidal form of the trees provides fewer suitable nest locations than would a similar stand of large, irregular shaped hardwoods. It should come as no surprise then that most natural nests were found in dominant hardwood trees. In the study area, hardwood species were almost always associated with mineral soils.

Similarly, the correlation between the poorly drained soils and the presence of plants such as american elm,

Table 1. NEST TREE AND SITE DATA

	<u>Nest Sites</u>						
	A	B	C	D	E	F	G
Nest type	natural	natural	artificial	art.	nat.	nat.	nat./art. ¹
Years used	1979	'79&'80	1979	'79&'80	1979	1979	1980
Nest Tree species	A. Elm	Larch	P. Birch	B. Ash	Y. Birch	B. Ash	B. Popular
N. T. canopy position	dominant	dom.	dom.	dom.	intermediate ²	dom.	dom.
N. T. age (years)	61	n/a ³	55	95	98	97	65
N. T. height (meters)	18.5	14	20	20.5	16.5	15.5	26.5
Average age of trees (years)	58.5	55.7	52.5	99.3	69.5	74.8	60.5
Average height of trees (m.)	11.4	10.3	12.8	13.6	15.7	8.5	12.6
Canopy cover (%)	6.5	43.5	5.75	19.5	9.0	39.75	5.75
Soil series	Cathro	Cathro	Shooker	Talmoon	Alstad	Alstad	Shooker
Habitat type	BC	BC	ew	ew	ew	ew	ew
	I	J	K	L	M	N	O
Nest type	nat.	nat.	nat.	art.	nat.	nat.	art.
Years used	1980	1980	1980	1980	1980	1980	1982
Nest Tree species	S. Maple	B. Popular	S. Maple	Basswood	Basswood	P. Birch	Larch
N. T. canopy position	dom.	dom.	dom.	dom.	dom.	overtopped ²	dom.
N. T. age (years)	83	72	87	72	68	n/a ³	125
N. T. height (meters)	21	25	19	24	17	5.5	13.5
Average age of trees (years)	80.5	68.25	75.8	62.3	60	66.7	122.2
Average height of trees (m.)	16.3	15.2	17.1	12.5	12.9	9.1	11.9
Canopy cover (%)	8	3	21.5	6.5	.86	3.75	27
Soil series	Alstad	Alstad	Alstad	Alstad	Alstad	Alstad	Talmoon
Habitat type	ew	ew	ew	ew	ew	ew	ew

¹ It was a natural nest in 1980. By 1982, an artificial nest was put in its place.

² These trees had lost their tops due to storm or wind damage.

³ These trees were too rotten to age with an increment borer.

Table 2. BASAL AREA FOR TREES (m2/ha)

Species	A	B	C	D	E	F	G	I	J	K	L	M	N	O	Total/species
<i>Abies balsamea</i>					.5		.2		3.5			.6	10.6		15.4
<i>Acer rubrum</i>	1.6		1.8					4.6	.8		4.3	13.1			26.2
<i>A. saccharum</i>								23.2		9.5	.1	.9			33.7
<i>A. spicatum</i>															.4
<i>Betula alleghaniensis</i>					3.4				7.9	7.3	1.3		6.7		26.6
<i>B. papyrifera</i>			5.7						1.2		1.2	.2	5.2		13.5
<i>Carpinus caroliniana</i>											.2				.2
<i>Fraxinus nigra</i>	6.8		1.0	16.2	24.1	5.6	13.4	.3	1.0	1.4	.2	4.1	1.0		75.1
<i>Larix laricina</i>		12.2												14.3	26.3
<i>Ostrya virginiana</i>										2.8	.8		1.4	.1	5.1
<i>Picea mariana</i>		.4													.4
<i>Populus balsamifera</i>							17.7		.7						18.4
<i>P. tremuloides</i>			1.9				.9								2.8
<i>Quercus macrocarpa</i>			2.8			2.0	1.1				.2	.2	.2		6.3
<i>Sorbus americana</i>		.1													.1
<i>Thuja occidentalis</i>				1.6					16.1						17.7
<i>Tilia americana</i>			9.3		.5		.8	7.7		16.6	20.4	4.7			60.0
<i>Ulmus americana</i>	9.0		4.6	9.1	2.1		5.8								30.0
Total/site	17.4	12.7	26.9	26.9	30.6	7.6	39.5	35.8	31.2	37.6	28.7	23.8	28.7	14.4	

Table 3. SHRUB LAYER COMPOSITION (Cover/Dispersion)

Species	Nest Sites														
	A	B	C	D	E	F	G	I	J	K	L	M	N	O	
<i>Abies balsamea</i>							1/1								
<i>Acer rubrum</i>	3/1		1/1			1/1	1/1					1/1			
<i>A. saccharum</i>								3/1		3/1	1/1				
<i>A. spicatum</i>							1/1		3/1	2/1	2/1		3/2		
<i>Actaea pachypoda</i>									1/1	1/1		1/1			
<i>A. rubra</i>									1/1	1/1		1/1			
<i>Alnus rugosa</i>		3/2				1/2									
<i>Amelachier sp.</i>					1/1										
<i>Aralia racemosa</i>								1/1		1/1	1/1				
<i>Betula papyrifera</i>						1/1									
<i>B. pumila</i>		2/2												2/2	
<i>Cornus alternifolia</i>								1/1							
<i>C. amomum</i>	1/1	1/2	1/1	1/1		1/1								1/1	
<i>C. rugosa</i>						1/1									
<i>Corvulus cornuta</i>			4/2			1/1	5/2		1/1	2/1	2/2	1/1			
<i>Fraxinus nigra</i>			1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1		
<i>Ilex verticillata</i>	2/2													1/1	
<i>Larix laricina</i>	1/1	1/1												1/1	
<i>Ledum groenlandicum</i>														1/1	
<i>Lonicera canadensis</i>									1/1						
<i>Ostrya virginiana</i>								1/1					1/1		
<i>Picea mariana</i>														1/1	
<i>Populus balsamifera</i>									1/1						
<i>P. tremuloides</i>			1/1			1/1	1/1					1/1			
<i>Prunus virginiana</i>			1/1	1/1			1/1		1/1		1/1				
<i>Quercus macrocarpa</i>			1/1			1/1	1/1				1/1	1/1		1/2	
<i>Ribes sp.</i>	1/1		1/1	1/1	1/1	1/1		1/1		1/1					
<i>Rosa sp.</i>														1/1	
<i>Rubus sp.</i>					1/1	2/3		1/1						2/2	
<i>Salix sp.</i>		1/2				2/2				1/1			1/1		
<i>Sambucus pubens</i>										1/1					
<i>Spirea alba</i>	1/1	1/2								1/2					
<i>Tilia americana</i>			1/1				1/1	1/1	1/1			1/1			
<i>Ulmus americana</i>			1/1	1/1	1/1	1/1	1/1	1/1							
<i>Vaccinium sp.</i>						2/3									
<i>Zizia aurea</i>					1/1										

The Daubenmire Cover Scale

Cover Class	Range of Cover (%)
6	95-100
5	75-95
4	50-75
3	25-50
2	5-25
1	0-5

Braun-Blanquet Degrees of Dispersion

- 5 = growing in large, almost pure population stands
 4 = growing in small colonies or forming larger carpets
 3 = forming small patches or cushions
 2 = forming clumps or dense groups
 1 = growing solitarily

Table 4. LEGEND.The Daubenmire Cover Scale

Cover Class	Range of Cover (%)
6	95-100
5	75-95
4	50-75
3	25-50
2	5-25
1	0-5

Braun-Banquet Degrees of Dispersion

- 5 = growing in large, almost pure population stands
 4 = growing in small colonies or forming larger carpets
 3 = forming small patches or cushions
 2 = forming clumps or dense groups
 1 = growing solitarily

* indicates that the plot was located near the center of the nest site.
 No asterisk indicates the plot was located near the edge of the nest site plot.

Table 4. GROUND LAYER COMPOSITION (Cover/Dispersion)

	Nest Site Plot Location																	
	A	A*	B	B*	C	C*	D	D*	E	E*	F	F*	G	G*	I	I*	J	J*
<i>Abies balsamea</i>																		
<i>Acer rubrum</i>	1/1				1/1	1/1												
<i>A. saccharum</i>															2/1	1/1		
<i>A. spicatum</i>													1/1	1/1			2/1	2/1
<i>Actaea sp.</i>																	1/1	2/1
<i>Allium tricoccum</i>													1/1					
<i>Amphicarpa bracteata</i>													1/1					
<i>Anemone cylindrica</i>					1/1								1/1					
<i>A. quinquefolia</i>					1/3		1/1				1/1	1/1	3/4				1/1	
<i>Anemone sp.</i>									2/1									1/1
<i>Aralia nudicaulis</i>					1/1							1/1	1/1				1/1	1/1
<i>Arisaema atrorubens</i>																	1/1	1/1
<i>Asarum canadense</i>					1/1						1/3	5/5	2/1	1/1	1/1	3/1	1/1	1/1
<i>Aster macrophyllus</i>																	1/1	3/2
<i>Athyrum filix-femina</i>																	4/1	1/1
<i>Betula alleghaniensis</i>																		1/2
<i>B. pumila</i>																		1/2
<i>Brassica sp.</i>				1/1					1/1	1/1								
<i>Caltha palustris</i>								1/1	1/1		1/1							
<i>Carex sp.</i>	5/2	2/2					1/2	4/2		2/2								
<i>Chamaedaphne calyculata</i>			1/1	2/2														2/2
<i>Circaea quadrangulata</i>																		3/2
<i>Clintonia borealis</i>																	1/1	1/1
<i>Coptis trifolia</i>																		1/1
<i>Cornus amomum</i>																		2/1
<i>C. canadensis</i>							1/1										1/1	2/1
<i>Corylus cornuta</i>							1/1			1/1							1/1	
<i>Dierwilla lonicera</i>																		2/1
<i>Dryopteris disjuncta</i>										1/1						2/1	1/1	1/1
<i>D. phaeopteris</i>																		
<i>Equisetum sp.</i>					1/1				1/1	1/1	1/1	1/1					1/1	
<i>Fragaria vesca</i>					1/1				1/1		2/2	1/1	1/1					
<i>F. virginiana</i>			1/1	1/1	1/1				1/1	1/1	1/1	2/3	1/1	1/1			1/1	1/1
<i>Fraxinus nigra</i>	1/1				1/1				1/1	1/1			1/1	1/1	1/1		1/1	1/1
<i>Galium sp.</i>	1/1		1/1		1/1	1/2			1/2				1/1	1/1	1/1		1/1	1/1
<i>Gentiana linearis</i>																		
<i>Gramineae</i>	3/1		1/1		1/1	2/2		1/2	2/2		4/2	2/2					2/2	1/2
<i>Hepatica americana</i>	3/1				1/3													
<i>Ilex verticillata</i>							1/1											
<i>Impatiens capensis</i>	1/1				1/1		1/1	4/2	1/1	1/1	1/1	1/1	1/1	1/1			1/1	1/1
<i>Ipomoea purpurea</i>																		
<i>Iris versicolor</i>					1/1						3/1							
<i>Larix laricina</i>																		1/1
<i>Ledum groenlandicum</i>			1/1	1/1														
<i>Lonicera canadensis</i>																	1/1	1/1
<i>Lycopodium lucidulum</i>																		
<i>L. obscurum</i>																		
<i>Lycopus sp.</i>																		
<i>Maianthemum canadense</i>	1/1			1/1	1/1						1/1	2/4	1/1	1/1		1/1	1/1	1/1
<i>Nasturtium officinale</i>							1/1		1/1	1/1								
<i>Nemophanthus mucronata</i>			1/1	2/2														
<i>Onoclea sensibilis</i>	1/1	1/1										2/4						
<i>Osmorhiza claytonii</i>								1/1										
<i>Panicum sp.</i>					1/1													
<i>Parthenocissus quinquefolia</i>								1/1	1/1									
<i>Polygonatum pubescens</i>					1/1								1/1	1/1			1/1	
<i>Polygonum sagittatum</i>																		
<i>Potentilla palustris</i>																		
<i>Prunus virginiana</i>					1/1								1/1	1/1				
<i>Pteridium equisetum</i>					1/1													
<i>Pyrola rotundifolia</i>																		1/2
<i>Quercus macrocarpa</i>													1/1	1/1				
<i>Ribes sp.</i>			1/1							2/1	1/1	1/1					1/1	
<i>Rosa sp.</i>																		

(Table 4. Cont. on next page)

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[illegible]

black ash, silky dogwood, jewelweed, and bedstraw that favor wet sites is to be expected. Other plants such as hazel, Canada mayflower, basswood, and sugar maple indicate a more mesic site (Coffman, Alyanak, and Resovsky, 1980). The Soil Conservation Service information confirms this site characterization. The abundance of wild strawberry suggests that much of the area has been disturbed (Coffman, Alyanak, and Resovsky, 1980). Old homesteads and logging operations in the area could account for the presence of strawberry. Present land use practices, as well, continue to disturb this area and adjacent regions in Aitkin County.

Plotting the nest sites on an air photo suggests a correlation between nest location and man-made openings such as power line right-of-ways, wildlife openings, and dirt roads. This is probably just a coincidence. The power company, road builders, and wildlife managers logically chose mineral soils in which to plant their poles and on which to drive their equipment. Unfortunately, the local loggers also seem interested in mineral soils since they support more valuable species of trees. Two nest sites that were to be included in this study were excluded since they had recently been logged.

If trees with nest structures were left alone or if artificial nests were erected, small scale logging in the area would probably have little impact on the owl's habitat. Information provided by the Soil Conservation Service provides a clue to a more serious threat to Great Gray Owl habitat. "This soil is well suited to grow cultivated farm crops if excess ground water is adequately drained." Developers in Aitkin County, acting on similar recommendations and economic considerations, have drastically altered thousands of acres in order to grow potatoes. The effects of scraping, ditching, and tiling are much more significant than that of logging. Then, of course, there is always the prospect of peat mining.

This study indicates the importance of mineral soils and stands of hardwoods to the nesting efforts of Great Gray Owls. This is, however, only one aspect of the bird's habitat. How much sedge meadow, tamarack swamp, or other cover type does it need for hunting? How critical is the availability of nest sites? Of course, more comprehensive raptor habitat studies have been conducted (Titus and Mosher, 1981). These studies were on birds who build their own nests and who both hunt and nest in similar habitats. New methods of investigation will have to be developed to adequately answer

questions about Great Gray Owl habitat.

Ideally, a habitat suitability index model should be constructed for the species. Such a model could be used to identify and protect appropriate owl habitat. I hope the information contained in this paper would prove useful in the construction of a habitat model for the Great Gray Owl. Until a more comprehensive study is conducted, forest cover type maps and soil surveys could be combined to find areas of high value to Great Gray Owls.

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Movement Strategies, Mortality, and Behavior of Radio-Marked Great Gray Owls in Southeastern Manitoba and Northern Minnesota¹

James R. Duncan²

Abstract.--Forty-three great gray owls (*Strix nebulosa*) were radio-marked in southeastern Manitoba and northern Minnesota. The movements and behavior of these birds revealed sex-biased mobility in a year of low prey availability and residency in a high microtine year. The great horned owl (*Bubo virginianus*) was the most significant predator in both situations. The adaptive significance of different life-strategies evolved in the great gray owl are discussed.

INTRODUCTION

Natural selection has operated on northern forest owls to produce numerous adaptations enabling their survival in boreal forest habitat. These include anatomical (i.e., wing shape and size) and behavioral (i.e., hunting methods) adaptations resulting from interactions with prey populations over an evolutionary time scale (Norberg 1987)¹. Mikkola (1983) noted a large degree of niche overlap among many northern forest owl species. He speculates that this lack of ecological isolation is due to the cyclic nature of their food and that, during years of low prey densities, the local sympatry of owls is not constant. Observable morphological and behavioral differences have arisen from interspecific competition and in response to a number of environmental constraints. Lundberg (1979) notes that nest-sites, food, clutch size, mate and nest territory fidelity, sexual dimorphism and longevity all help shape the pattern of mobility and wintering strategies of northern forest owls. Of these, food abundance and nest-site availability are considered the most prominent (Lundberg 1979, Nero 1980, Mikkola 1983) and are thought to interact as follows:

a) There should be selection for year-round residency of both sexes in hole-nesting (scarce resource) food generalists.
e.g. ural owl, *Strix uralensis*: (Lundberg 1979; Saurola 1987¹).

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e.g. barred owl, *Strix varia*: ¹(Nicholls & Fuller 1987).

b) Both sexes should be migratory if nest-sites are abundant but a dependence exists on a highly fluctuating food source (voles).
e.g. long-eared owl, *Asio otus*: (Lundberg 1979).

c) In hole-nesting food specialists, resident males and migratory females should be selected for.
e.g. boreal owl, *Aegolius funereus*: (Lundberg 1979, Korpimäki 1986a).
northern hawk-owl, *Surnia ulula*: (Byrkjedal & Langelille 1986; Sonerud 1986).

Lundberg (1979) concluded that assured access to a nest-site is probably the most fundamental factor governing movement patterns in northern forest owls. Therefore, the ural and barred owls residency is presumably an adaptation to the scarce nature of their nesting structure and is facilitated by their generalistic diet. The relative abundance of stick nests allows the long-eared owl to migrate to snow-free areas, and is required because of its specialized small mammal diet. A conflict arises between migration (specialist diet) and residency (scarce suitable nest-holes) for the boreal and northern hawk-owls. Here, males should remain resident for as long as possible and females should move to areas of greater prey densities or vulnerability (Lundberg 1979). Sonerud (1986) stated that the above arguments can be reversed whereby the nesting site is determined by a) feeding ecology, b) hunting habitat, and c) the effect of snow cover on prey vulnerability.

While all owls can hunt by the energetically inexpensive sit-and-wait mode, some, like the long-eared owl, use the energetically more expensive quartering (flying) hunting method. During snow-free periods both hunting methods can take advantage of prey occurring in clear-cuts

and similar openings. Sonerud (1986) determined that because of snow cover the less abundant small mammal populations occurring in forest habitat are more vulnerable to predation than the more abundant populations occurring in open areas. This is due to increased supra-nivean and snow-tunneling activity of small mammals in the former habitat resulting from the lack of a well developed, continuous, pukak layer (space formed at the snow-ground interface). Short and broad wings, providing greater maneuverability among vegetation, are but one of many adaptations enabling certain forest owls to capture prey in wooded habitat (Norberg 1987)¹. The relatively long and narrow wings of the long-eared owl renders it less able to capture prey in forest habitat. It must migrate to snow-free areas and return only when open areas are partially snow-free. By this time presumably only old stick nests are available. Long-eared owls will use nest-holes (nest boxes) on rare occasions when competitors are absent (Cave 1968 in Sonerud 1986). Ural and barred owls can remain year-round residents by their ability to locate and capture prey by the sit-and-wait hunting mode in forest habitat. Their year-round residency is facilitated by their ability to survive on alternate prey items when small mammal populations are at a cyclic low. Northern hawk-owls and boreal owls also employ a sit-and-wait hunting strategy, enabling them to reside year-round in forest habitat where the small mammals on which they specialize are more vulnerable during periods of snow cover. However, during periods of low small mammal densities, they are less able to switch to alternate prey than are ural and barred owls. Observed male residency of northern hawk-owls and boreal owls perhaps indicates that the potential reproductive benefits of possessing a suitable nest structure outweigh the risk of winter starvation (Lundberg 1979).

The great gray owl (*Strix nebulosa*) is quite catholic in its use of habitat and nest structures, but it is a small mammal specialist and is therefore similar to the long-eared owl (Collins 1980, Nero 1980, Mikkola 1983, Roselar 1985 and Korpimäki 1986b). According to Lundberg (1979) it should be migratory, but Sonerud (1986) argues that given adequate prey it should exhibit year-round residency since, like the boreal and northern hawk-owls, it can hunt within forest habitat and catch concealed prey. However, normal microtine populations can decline to extremely low densities at unpredictable intervals, and can subsequently fail to recover for long periods of time (Mihok et al. 1985). During such declines we may predict age and sex biased mobility as was reported for northern hawk-owls by Byrkjedal & Langhelle (1986). These predictions arise from three "single-factor" hypotheses reviewed by Ketterson & Nolan (1983) and discussed in Byrkjedal & Langhelle (1986).

a) Body Size Hypothesis: larger birds endure fasting better than smaller ones and therefore are in less need of migrating (which may imply a mortality risk).

b) Dominance Hypothesis: subdominant birds are relegated to adverse habitats due to intraspecific competition and are the first to move when conditions get harder.

c) Arrival-time Hypothesis: the sex that establishes the breeding territory should migrate the shortest distance in order to get early access to a territory in spring.

In this paper I shall examine the movements and behavior of radio-marked great gray owls in relation to the above hypotheses and compare those of other northern forest owl species. The adaptive nature of the different life-strategies evolved in these species will be discussed.

MATERIALS AND METHODS

1. Radio-telemetry

Forty-three great gray owls were radio-marked in southeastern Manitoba and northern Minnesota between April 1984 and August 1986. This area is primarily boreal forest. Two locations, A & B (fig. 1), approximately 100km apart, are currently being experimentally managed for this species in light of existing and potential threats to habitat. Both locations contain large stands of old and mixed-age growth tamarack (*Larix laricina*) and tamarack/black spruce (*Picea mariana*) with natural and man-made openings, i.e., burns and clear-cuts. The owls radio-marked within the study area, all of figure 1, may be described as three samples:

a) April-July 1984: eight mated pairs, a breeding male, and 11 of their progeny. Radio-marked at location A, figure 1 (Loch 1985)³.

b) February-March 1986: three immature (hatch-year 1985) males, two adult females, and an adult male. Radio-marked at various locations within the study area, figure 1.

c) June-August 1986: a breeding pair, two breeding females, and five of their progeny. Radio-marked at location B, figure 1.

Radio-transmitters measured 8cm long by 15cm in diameter and averaged 35g complete with harness. A 28cm long whip antenna extended posteriorly from each unit. Each transmitter was powered by a 2000 milliamper, 3.9 volt lithium battery; current drain ranged from 0.10-0.19 milliamper/hour. Frequencies were separated by at least 15khz within the 164 megahertz band. A modified "back-pack-type" harness, consisting of a plastic coated wire running through 6mm (diameter) of teflon tubing, was developed by Loch (1985)³ to attach transmitters to owls. Properly fitted, the transmitter and harness

³Loch, S. L. 1985. Manitoba great gray owl project progress report. April 1, 1984 to August 1, 1985. Manitoba Dept. of Nat. Res., Winnipeg, Manitoba

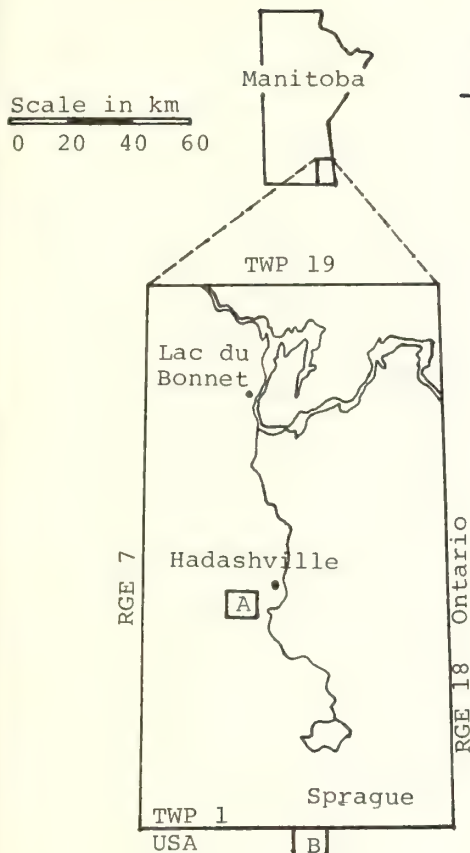


Figure 1.--The study area including two locations, A and B.

lay adjacent to the owl's skin and was completely covered by its plumage. Only the antenna protruded out over the bird's tail.

Owls from sample A and C were snared from perches at or near their nests using a hand-held fiberglass telescoping pole. Some juveniles were captured by hand or with a verbaile trap baited with live mice. Owls from sample B were caught along roads using either an artificial or live mouse to lure them close enough for capture in a large, hand-held, fish-landing net (Nero 1980).

From the ground, two or more compass bearings for an individual radio-marked owl enabled its location to be plotted on a map or air photo. Bearings were obtained with a three or four-element, directional hand-held yagi antenna connected to a radio-receiver via a RG-59/U coaxial cable. Radio-signals were detected from as far as 10km with factors such as owl perch height, local topography, signal interference and seasonal changes of deciduous vegetation affecting detection range. When radio-contact from the ground was lost, indicating the owl may have moved out of radio-reception range, an attempt to relocate the owl via aircraft was made. For this purpose a four-element directional yagi antenna was

mounted to each wing of a fixed wing mono-plane. The antenna's elements were positioned vertically and the antennas pointed outward, perpendicular to the flight path. A right-left switch connected both antennas to the receiver via RG-59/U coaxial cables. Search patterns were determined by the last known location of the missing owl, topography and aerial reception range (55-135km at 2500m above ground level). When a signal was detected the owl's location could be determined to within 50m by a number of low level (40m above ground) passes. When weather or fuel constraints prohibited the above, the owl's approximate location and/or bearing was obtained to facilitate relocation, either by aircraft or from the ground, at a later date.

The locations of radio-marked birds were obtained at varying time intervals until their transmitters expired, mortality occurred, or radio-contact was lost. An owl's movements are herein defined as the linear distance between locations as determined by the radio-telemetry techniques mentioned above. These movements represent a minimal value as the owl may have meandered or made detours while enroute between locations.

Recapture attempts were made to remove or replace transmitters about to expire. Signal changes, such as decreased reception range, frequency drift, and orientation of the yagi antenna, indicated possible mortality. Prompt recovery of the transmitter and owl remains was required to determine the cause of death, but was not always possible. The cause of mortality was a subjective decision based on sign such as tracks, feces, feathers, pellets, and teeth marks. Owls with whom radio-contact was lost were searched for on all subsequent search flights until their transmitter's expected expiry date.

On occasion, especially for sample c, the radio-marked owls' behavior was noted. Dense vegetation only rarely prohibited viewing the owls from sufficient distances so as not to disturb them.

2. Small Mammal Census

Locations A & B (fig. 1) were censused for small mammals during the spring (May 21 to June 2, 1986) and fall (October 14-22, 1986). The census at each location consisted of six lines, in three pairs, of 50 stations per line with 10m spacing between the stations of a line. A pair of census lines ran parallel and were 50m apart. One museum special snap-trap, baited with peanut butter, was set at each station for three nights. The lines were checked each morning, trapped mammals removed and traps reset or re-baited as required. In each location, A & B (fig. 1), a pair of census lines sampled a tamarack stand, while the other two pairs sampled open areas containing suitable perches. These areas were used by hunting owls (Servos 1985, Duncan unpubl. data).

RESULTS

Movements

1. Sample A

Recorded post-breeding movements of adults showed sexual differences with respect to the magnitude and chronology. Six of seven adult females left their breeding grounds (i.e., moved at least 10km away and did not return) between October 1 and December 20, 1984, while only one of eight adult males had done so. This difference was significant ($P = 0.0089$, one-tailed Fisher exact probability test, Daniels 1978). All birds had left the area by February 22, 1985. Exact departure dates are not known due to intervals between radio-checks. Only four young owls survived long enough to leave their natal home range and did so prior to December 20, 1984.

Eight adult owls were located on their 1985 summer home ranges. Distances from their 1984 breeding home ranges were 0, 41, 172, and 325km for males and 360, 416, 521, and 684km for females. The average distance for males was significantly less than that for females ($P < 0.05$, one-tailed Mann-Whitney U test, Daniels 1978).

Other owls made substantial movements before radio-contact was lost or mortality occurred. One adult female died on her 1984 breeding home range; three others had moved 15, 164, and 494km before radio-contact was lost. One adult male died on his 1984 breeding home range, two died 77 and 98km away, and two had moved 141 and 398km before radio-contact was lost. Seven young owls died on or within 10km of their 1984 natal home range prior to September 28, 1984. The remaining four died 13, 62, 83, and 102km from their natal home range prior to February 19, 1985. Figure 2 shows a simplified map with movements described above. There were no coordinated movements between males and females of breeding pairs.

2. Sample B

Recorded movements of six late winter-caught owls also suggests some sexual differences in movement patterns. Three of four males, one adult and two immatures (hatch-year 1985), remained within 2km of their capture site.

- An adult male died less than 1km from where it was caught 44 days earlier. It had starved to death, suspended 1m above the ground with its wing wedged in a forked branch.

- An immature male remained within 2km of its capture site for 200 days. Its remains were found adjacent to an active trap line.

- An immature male has remained within 4km of its capture site to date (381 days).

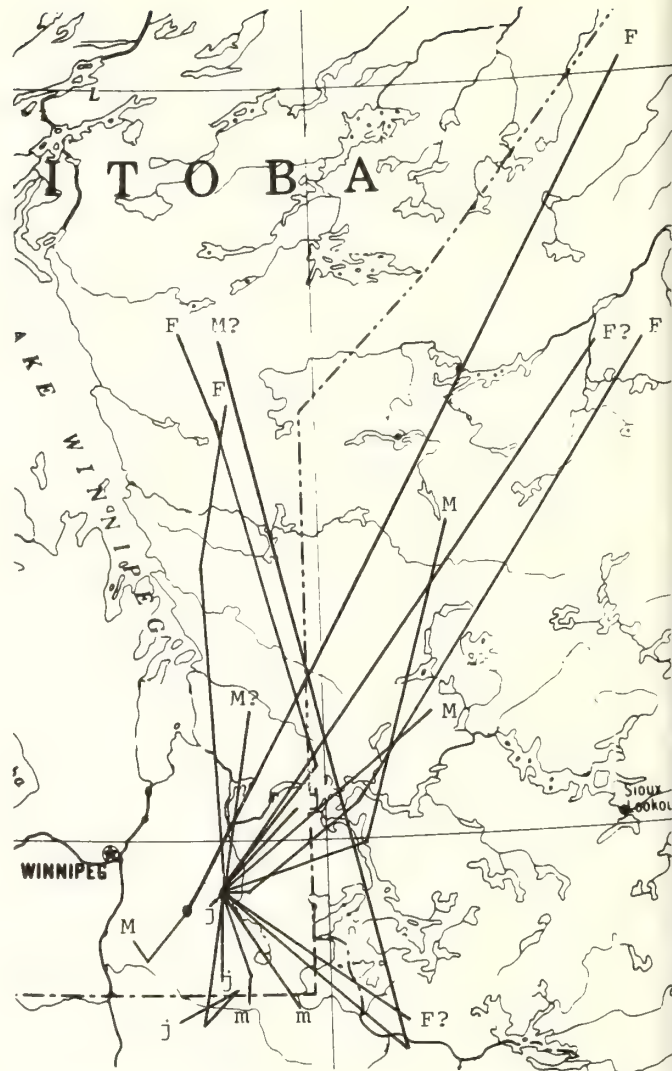


Figure 2.--Recorded post-breeding movements of radio-marked great gray owls: M and F indicate male and female, respectively, on summer 1985 home ranges. A ? denotes last known location of a bird. An m or j marks where mortality occurred for males and juveniles, respectively. Birds are from sample A.

The remaining three owls moved relatively soon after they were radio-marked.

- An immature male moved 112km north 30 days after capture.

- An adult female moved 26km northwest 30 days after capture and was missing 12 days later. Subsequent search flights failed to relocate this owl.

- An adult female moved 21km northeast 12 days post capture. Nine days later it was 112km southeast where its transmitter, but few remains, were recovered.

Table 1.--Suspected cause of mortality of 23 radio-marked great gray owls in southeastern Manitoba and northern Minnesota.

Sample ¹	great horned owl	malnutrition	lynx	fisher	trapped	hunting accident	unknown
A	9	2	2	2	0	0	0
B	0	0	0	0	1	1	1
C	4	0	0	1	0	0	0

1. See methods for description of samples.

3. Sample C

One of two surviving young, a female, moved 118 north on November 28, 1986. Its sibling, and a pair of adults, remain to date within 5km of their 1986 natal and breeding home ranges respectively. The 5 owls, whose remains and transmitters were recovered, all died within five to 10km of their breeding or natal home ranges from August to November 1986.

Mortality

Table 1 shows the suspected cause of mortality for those owls whose remains and transmitters were recovered. This does not include six owls with whom radio-contact was lost. Since these instances may involve mortality in which the transmitters ceased functioning (i.e., shot or bitten through), values in table 1 are minimal. The 13 great gray owls killed by great horned owls (*Bubo virginianus*) consisted of two adult females, three adult males, and eight young. Malnutrition was the only suspected cause of death in two cases, both involving young birds, however it most likely was a factor in other cases (see discussion). Lynx (*Lynx canadensis*) apparently took two young owls. Fisher (*Martes pennanti*) took one adult female and two young owls. The fate of the remaining three owls (sample B, table 1) was described above.

Small Mammal Census

Table 2 shows an expected increase in the abundance of small mammals in both locations from spring to fall. Location B had the highest abundance for both the spring and fall. The high percentage of red-backed voles (*Clethrionomys gapperi*) in the fall sample (table 2) was also noted for two other independently sampled areas within the northern and eastern portions of the study area denoted in figure 1 (W. O. Pruitt Jr.⁴ and S. Mihok⁵, pers. comm.).

⁴Pruitt, W. O., Jr. 1986. Personal conversation. University of Manitoba, Winnipeg, Manitoba.

⁵Mihok, Steve. 1986. Personal conversation. Pinawa, Manitoba.

⁶Loch, Steve L. 1985. Personal conversation. Foley, Minnesota.

DISCUSSION

In 1984, 19 active great gray owl nests were found in southeastern Manitoba and adjacent Minnesota (Nero, unpubl. data). More than 100 man-made nest structures, covering a linear distance of more than 200km, and including locations A & B (fig. 1), were checked from April to June 1985. None were occupied. Coupled with similar negative results from Minnesota (S. Loch⁶, pers. comm.) it appeared that the vole crash within the study area in the winter 1984-85 (S. Mihok⁵, pers. comm.) carried over into the spring and summer. This suggested that the emigration of great gray owls from southeastern Manitoba (fig. 2) was general and/or birds remaining (i.e., the two adult males, sample A) lacked the stimulus to breed. Movements of owls on summer ranges in the north (fig. 2) suggested that breeding had not occurred there either (Loch 1985)³. However, three of eight great gray owls caught from January to March 1986, plus a road-killed owl, were from the 1985 hatch-year. This suggested that considerable reproduction had taken place within the study area or that new birds had moved in. In 1986, location B (fig. 1) contained the only active great gray owl nests found, which coincided with its moderate spring small mammal population (table 2).

Coinciding with the 1984 generalized microtine crash, adult female great gray owls left their 1984 breeding grounds earlier, and travelled farther, than adult males. Given that the male great gray owl establishes the breeding territory (Nero 1980, Mikkola 1983) the observed adult sex-biased mobility

Table 2.--Abundance indices of small mammals for two locations, spring and fall.

Location ¹	Spring		Fall	
	A	B	A	B
Index ²	1 ³	10	24	43
% <i>Microtus</i> sp.	0	70	12	21
% <i>Clethrionomys</i> sp.	0	19	65	43
% Soricidae	86	6	23	28
% Others	14	5	0	2
Sample size (N)	7	84	217	383

1. See figure 1.

2. Index, $I = (100 \cdot N) / D$, N = total # caught and D = # traps * # nights.

3. $D = 885$, all others $D = 900$.

pattern would be best explained by the arrival-time hypothesis. This is further supported by the return of one male to occupy an expanded version of its 1984 breeding home range after wintering 40km north. Another male settled into a 1985 summer home range 41km west of its 1984 breeding home range. The greater distances travelled by females, and their earlier departure, apparently contradicts predictions of the body size and dominance hypotheses.

Four young owls from sample A survived long enough to leave their 1984 natal home ranges and did so prior to adult males but concurrently with adult females. Perhaps these young owls are influenced more by social dominance and they are the first to move when conditions get harder. Subsequent mortality of these owls before they could establish 1985 summer home ranges prevents comparisons with the eight adults that did. The high mortality observed (table 1 and results) may have resulted from the young being relegated to poorer habitats. Predators, especially the great horned owl, and malnutrition were the only suspected cause of mortality of owls from sample A. These two factors are probably interrelated and tied in with the small mammal crash. Hungry or starving owls, concentrating on catching prey would be less wary of potential threats. Perhaps the microtine population was insufficient to provide a long enough "training period" to enable the young owls to fully benefit from their inherited extreme ear asymmetry (Norberg 1987)¹. This adaptation, which enables owls to audibly detect and locate prey in dense ground vegetation or under snow, may prove to be a formidable handicap in such situations. Furthermore, a bird moving through unknown habitat would be at a disadvantage when it encountered resident predators. Loch (1985) postulated that following a 10-year cyclic peak in populations of ruffed grouse (*Bonasa umbellus*) and snowshoe hare (*Lepus americanus*), the resulting large population of seasoned predators, i.e., great horned owl and lynx, would broaden their search image to alternate prey species, including the great gray owl. Despite a high fall 1986 microtine population (table 2), predator-related mortality, particularly great horned owl, was high (table 1). Mikkola (1983) notes one instance of the eagle owl (*Bubo bubo*) killing the nominate European subspecies of the great gray owl (*S.n. lapponica*). In North America the great horned owl appears to be a more significant predator of the great gray owl than is the eagle owl in Eurasia.

Movements of great gray owls radio-marked in February and March 1986 (sample B) suggested sexual differences in mobility as well. Males tended to be relatively sedentary compared to females. The adult females' greater mobility at this time may represent a search for males with territories conducive to breeding. The three adult owls, a male and two females, were observed spending much time on high and exposed perches, with frequent flights over tree tops. These may be activities related to spring courtship.

The virtual lack of movements by the radio-marked owls (from sample C) from their 1986 natal and breeding home ranges is most likely due to the increased abundance of their principle prey, voles (table 2). The five owls that died were within 10km of their natal or breeding home ranges. The one exception, a young female, moved 112km north; her sibling remained on their natal home range. This is an enigma, given the amount of suitable habitat and ample prey en route to where she relocated.

Movements of owls from sample B & C were of lesser magnitude than those of sample A (fig. 2), which relocated the majority of owls outside the study area denoted in figure 1. Kerlinger & Lein (1986) found that social dominance alone may explain the winter distribution of snowy owls (*Nyctea scandiaca*). Byrkjedal & Langhelle (1986) related age and sex differences in hawk-owl mobility to two "single factor" hypotheses. Males are more influenced by competition for nest-sites, while females and juveniles, which leave the breeding grounds, may be more influenced by social dominance. Great gray owls seem to parallel the hawk-owl and boreal owl in this respect, at least during times of low prey availability.

Byrkjedal & Langhelle (1986) note that nest-site availability is probably less critical for the hawk-owl, as it is for the boreal owl. The great gray owl is probably the least affected by nest-site availability. However, adult males of all species would benefit by remaining at least within the breeding range to sample food and potential nest-sites (Byrkjedal & Langhelle 1986). Furthermore, given an adequate food supply, it would possibly benefit successful pairs to remain together into the next breeding season, on or near their former breeding territory. A pair of great gray owls that fledged two young in 1986 remained together throughout the winter on their breeding home range. In mid-March 1987 the female was observed following the male, soliciting food from him with barely audible vocalizations similar to the begging calls of the young.

Numerous half to 2 day visits by adult breeding females to neighbouring family groups up to 4km away were documented in the post-fledging period during the 1986 breeding season. During this period the male feeds the young directly (Nero 1980, Mikkola 1983). Similar, but briefer visitations by female flammulated owls (*Otus flammeolus*) was reported by Reynolds & Linkhart (1987). If a female's previous year's mate has not survived to the following year, then an awareness of adjacent males and/or breeding territories would expedite successful reproduction the following year. Reynolds & Linkhart's (1987) study of nest-site and mate fidelity in flammulated owls lends support to this idea. Mikkola (1983) gives several examples of pairs that have bred (or at least have stayed) together for 2 or even more consecutive years at the same nest-site, while voles were scarce in some instances. Recaptures of two banded adult females (Nero, unpubl. data), each nesting three times

within the same immediate breeding area, over a 10 and 7 year period respectively, documents nest-site fidelity in this species.

Evidence of fall territoriality and nest inspections (Duncan, unpubl. data), together with the above data, suggests year-round residency to be an adaptive behavioral strategy for great gray owls. Winter (1987¹ and pers. comm.) found great gray owls in Yosemite National Park, California, using pocket gophers (*Thomomys botta/monticola*) as maintenance prey items, enabling year-round residency, but not breeding, during cyclic lows in microtine populations. In Oregon, Bull & Henjum¹ (1987) found the maximum distance that 16 adult radio-marked great gray owls ranged from their nests, over 1 to 3 years, averaged 13km (+11). Movements of these birds, living in mountainous terrain, was thought to be a function of topography, with owls travelling short distances to change elevation, snow depth, and prey vulnerability. For great gray owls in southeastern Manitoba to accomplish the same, greater distances must be travelled, at least during years of low microtine populations (i.e., 1984-85). Movements of radio-marked adults north (fig. 2) actually placed birds at lower elevations, and possibly in locations of lesser snow depths and/or greater prey vulnerability.

The great gray owl's larger size and weight (Mikkola 1983) should make it even more likely to be a year-round resident than the smaller and lighter boreal and northern hawk-owls. These three species occupy the same range- the boreal forest -and are potentially strong competitors. Snow accumulations partially protect voles from these predators but the least affected is the great gray owl (Korpimäki 1986b). Their large size and peculiar habit of snow-plunging enables them to regularly catch voles through even hard snow layers up to 50cm deep (Collins 1980, Nero 1980, Korpimäki 1986b, Duncan, unpubl. data). The great gray owl's larger body mass should be more efficient at thermoregulation and better able to withstand temporary food shortages than its smaller competitors, even though a larger body requires more food (Korpimäki 1986b). The lower critical temperature, i.e., the point below which body temperature cannot be maintained without increased heat production, declines as body size increases. Therefore, the metabolic rate of a larger animal starts increasing at a lower temperature than is the case for a smaller animal. Also, a larger bird takes longer to starve to death (Peters 1983 in Korpimäki 1986b).

The various adaptations, both anatomical and behavioral, discussed above maximize the ability of great gray owls to achieve residency for as long as possible. These are means which minimize the destabilizing influence of dependence on a wildly fluctuating prey base.

¹Winter, J. 1987. Personal conversation. 5331 El Mercado Parkway, Santa Rosa, California.

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Summer Habitat Use by Great Gray Owls in Southeastern Manitoba¹

Marla C. Servos²

Abstract.--Sixteen radio-marked great gray owls, *Strix nebulosa*, were monitored from 27 June to 28 August 1984 to determine summer habitat use in southeastern Manitoba. Owls showed a strong preference for tamarack bogs, but other wet, open areas with adequate perches, such as treed muskeg habitats were also selected. Factors influencing habitat selection include availability of prey species (meadow voles and bog lemmings), suitable perches, cover, and shrub density.

INTRODUCTION

Great gray owls are generally rare across most of their range and their nomadic nature makes them difficult to study. Knowledge of the great gray owl's preferred habitats is limited although there is evidence of a preference for black spruce-tamarack bogs in Manitoba, for mature poplar stands near muskeg in Alberta and for mature old forests in California (Nero 1980). A better understanding of the preferred habitats of great gray owls is an important first step in the effective management of this species.

In the spring of 1984 six pairs of great gray owls nested in a small area of southeastern Manitoba, approximately 70 km east of Winnipeg. This large number of breeding owls in a relatively small, easily accessible area presented a unique study opportunity. As part of a continuing great gray owl research project by the Manitoba Wildlife Branch, 18 owls were radio-marked in the spring of 1984. This study focused on the summer habitat use of these radio-marked owls.

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MATERIALS AND METHODS

Study Area

The study area was located in southeastern Manitoba, approximately 70 km east of Winnipeg in the Sandilands Provincial Forest. The 1942 ha study area lies within the Manitoba Lowlands section of the Boreal Forest Region which is noted for its flat, poorly drained land with the predominant vegetation consisting of patches of black spruce and tamarack interspersed with swamps and meadows (Rowe 1972). Jack pine and trembling aspen are found on the drier areas.

A large portion of the study area was covered by tamarack bog (TL100) and five occupied nests were located on the edge of, or within this habitat type (fig. 1; habitat codes are described in table 1). The southern portion of the study area was the driest and its habitat types were composed mostly of jack pine, black spruce and trembling aspen. The wettest habitat types, the marsh muskeg (MARMUS), treed muskeg (TREMUS), class-0 (an old burn area), and tamarack bog (TL100), ran from the northwest corner diagonally across the middle of the study area and occupied the largest area. The northern portion was a relatively dry area composed mostly of young jack pine and trembling aspen with a thick shrub undergrowth.

Radio-telemetry

Eighteen great gray owls nesting in the study area were radio-marked during spring 1984 as part of a larger project of Dr. R.W. Nero, Manitoba Department of Natural Resources. Two of these birds were

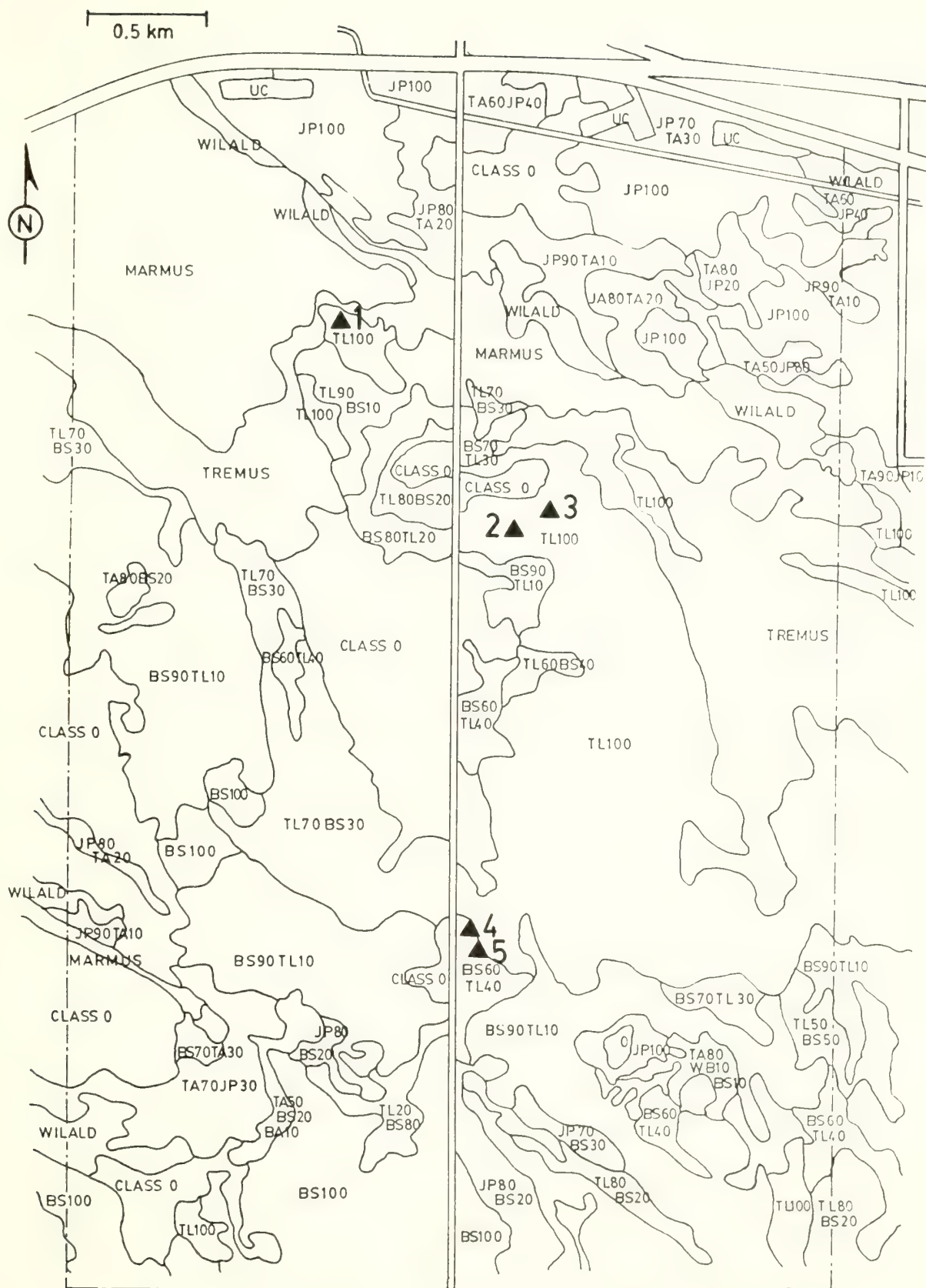


Figure 1.--Habitat types and nest locations in the the study area. ▲- occupied nest

eliminated from the study due to mortality. Sixteen radio-marked birds, five males, five females and six juveniles, were used to determine summer habitat selection. Radio-telemetry readings to determine the locations of the owls were taken on 31 different days from 27 June 1984 to 28 August 1984 and at all times of the day. The location of each owl, as determined by triangulation, was plotted on 1:15,840 scale air photos and each location was assigned to a habitat type defined using 1980 forest inventory maps. The receiving equipment consisted of an AVM Model LA-12 radio-tracking receiver and a four element, hand-held, 164 MHz Yagi antenna. The transmitters ranged in frequency from 164.014 to 164.842 MHz. The accuracy of this radio-telemetry equipment was on average 11 degrees.

Analysis was done on 608 owl locations. Radio-telemetry locations for individual birds were plotted and copied onto transparencies to be overlaid on the habitat map. The method for analyzing utilization-availability data described by Neu et al. (1974) and Byers et al. (1984) was employed. A chi-square goodness-of-fit test was used to determine whether there was a significant difference between the observed frequency of habitat use and the expected use of those habitats based on their availability (Byers et al. 1984). Bonferroni confidence intervals were then used to determine whether a specific habitat type was preferred or avoided.

The chi-square goodness-of-fit test was applied on all the data combined; on the data grouped by male, female, young; on the data grouped by month (June, July, August); and on the data grouped by time of day (morning: 0500-1100; afternoon: 1100-1700; evening: 1700-2300; night: 2300-0500). If the null hypothesis was rejected for any of the above cases, Bonferroni confidence intervals were calculated and compared for each habitat type.

Table 1.--Shortened codes for habitat designations.¹

Code	Description
BS	black spruce
TA	trembling aspen
TL	tamarack
JP	jack pine
Class-0	old burn
MARMUS	marsh-muskeg
WILALD	willow alder
TREMUS	treed muskeg

¹e.g. TL90BS10 describes a 90% tamarack-10% black spruce habitat.

Vegetation Analysis

As a check on the forest inventory maps, vegetation analysis using the point-centered quarter method (Cotton and Curtis 1956) was conducted on seven habitat types: five of the most common habitat types used by the owls and on two areas where the owls were never found. At each sampling point canopy cover was estimated ocularly, ground cover estimated using a 1 m x 1 m quadrat and shrub density (# stems/m²) was estimated using a 2 m x 2 m quadrat. Plants greater than 1 m in height were classified as shrubs and those less than 1 m were defined as ground cover.

Prey Abundance and Use

Small mammal trapping was conducted during July and August 1984 to determine relative abundance in the seven habitat types where vegetation analysis was done. Thirty Museum Special traps were set each night for three nights and were baited with peanut butter and rolled oats. The traps were set 10 m apart on randomly selected transects. The transects were moved after each trap night to reduce bias caused by variation within the habitat types. To determine what prey species the great gray owls were using, 110 owl pellets were collected in the study area from nests and roost sites from May to August 1984; dried and the skeletal remains were extracted for identification.

RESULTS AND DISCUSSION

Owl Pellet Analysis and Small Mammal Trapping

Analysis of the owl pellets collected on the study area revealed that the majority of the great gray owls' diet was composed of meadow voles (Microtus pennsylvanicus, 64%) and northern and southern bog lemmings (Synaptomys borealis and S. cooperi, 28%). Other species taken included mice (Family Cricetidae, 5%), red-backed voles (Clethrionomys gapperi, 2%) and songbirds (1%).

Meadow voles, red-backed voles and shrews were caught in all seven habitat types. Bog lemmings were caught only in the 90% tamarack-10% black spruce (TL90BS10), treed muskeg, 90% black spruce-10% tamarack (BS90TL10) and the 80% jack pine-20% black spruce (JP80BS20) habitat types. Deer mice (Peromyscus maniculatus) and meadow jumping mice (Zapus hudsonius) were caught only on the driest habitats, JP80TA20 and JP90TA10. More meadow voles than any other species were caught in the pure tamarack, class-0 and treed muskeg habitats.

Habitat Selection

All 16 radio-marked owls remained in, or within 0.5 km of the study area for the duration of the study. By 27 June 1984 all young owls were out of the nest and able to move from tree to tree although not yet flying. The male and female owls at nest 1 remained in the nest area and were seldom found on the east side of the forestry road. Both owls appeared to occupy the same range and frequented the TL100, TL90BS10 habitat types and the edges of the marsh-muskeg. The young owls and the male at nest 2 were always found on the east side of the road near the nest site in the TL100 habitats and in the areas with a high percentage of tamarack trees. The female from this family group apparently had dissociated from the male and young and was found mostly on the west side of the road. The family group from nest 3 followed a similar pattern. The ranges of the male and young from nest 2 and 3 overlapped as did the ranges of the female owls.

The owls from nest 4 and 5 moved north of their nest sites. The young and male of nest 4 were found in the same area, on the east side of the road, generally in the tamarack bog (TL100) although the male ventured further east than the young. The female from nest 4 was found in the same area as the male and young but also used the class-0 habitat on the west side of the road. The male and female of nest 5 were generally found on the west side of the road in the class-0 and TL70BS30 habitats. Fixes on the young of this nest, done only twice due to transmitter problems, placed the bird on the west side on the edge of the class-0 habitat.

The home ranges of the male owls from nests 2, 3 and 4 appeared to overlap. The range of the male from nest 5 overlapped with the nest 4 male and approached the range of the other males. The nest 1 male occupied an area in the northwest part of the study area and its range did not appear to overlap with the others.

The chi-square goodness-of-fit test on the radio-telemetry data lead to the rejection of the null hypothesis since the chi-square test value was larger than the chi-square table value in all cases. Thus the owls were not entering the different habitats by chance alone but were selecting or avoiding certain habitat types. Bonferroni confidence intervals applied for each habitat type showed a strong preference for the pure tamarack bog (TL100) by males, females and young, during August and during all time periods (table 2). Overall, the class-0 (old burn), the treed-muskeg (TREMUS) and the 90% tamarack-10% black spruce (TL90BS10) habitat types were also selected. Although these results can not explain why the owls

are selecting these habitats, possible explanations can be suggested as to why great gray owls select certain habitat types in preference to others.

The great gray owls in this study area showed a strong preference for pure tamarack bog areas. The tamarack bogs were generally free of a dense shrub layer (shrub density 0.45 stems/m²) and the ground cover was mostly low-growing mosses and grasses. These vegetation characteristics would make it easy for the owls to locate and capture their prey. The horizontal growth of the tamarack branches would provide suitable perches. Although the average canopy cover was only 35%, this habitat would appear to provide sufficient concealment and cover for the young owls. This habitat also supported their preferred prey species, the meadow vole.

The 90% tamarack-10% black spruce (TL90BS10) habitat type was selected by females, used by males, but not used at all by young. This habitat was also selected by all owls overall in August. Except for the lack of shrub growth, this habitat was similar in vegetation characteristics to the pure tamarack bog and therefore was probably a preferred habitat for the same reasons. Both bog lemmings and meadow voles, which made up the largest portion of the diet of these owls, were caught in this habitat type.

The class-0 habitat type was an old burn area and was preferred by female owls but was not selected or avoided by males and young. Class-0 habitat was also selected by the owls in July. This preference by females, especially in late summer, may indicate a dissociation of the females from the family group. Since the male owls continue to feed the young long after they are out of the nest (Nero 1980), the females may move to other hunting areas. The class-0 habitat would appear to be favourable for hunting activities. More meadow voles than any other species were trapped in this habitat type. Dead trees left standing after the burn were scattered throughout the area and provided good perches for hunting. Although the shrub growth was more dense here than in the tamarack bog, the shrubs were generally concentrated in clumps, leaving areas of unimpeded access to prey on the ground. Black spruce are regrowing in this habitat but do not yet form a canopy, allowing for unhindered flight through the lower vegetation. But this lack of canopy cover would provide little or no shade or concealment and may explain why the males with the young did not select this habitat type.

The treed muskeg (TREMUS) habitat was preferred by the great gray owls although there was no significant selection in the

Table 2.--Summary of the Bonferroni confidence intervals. $P < 0.05$ $df = n/K - 2$
S-selected A-avoided 0-zero frequency of use
N-no significant difference @-see table 3

DATA GROUPINGS											
Habitat	Overall	By sex (age)			By month			By time of day			
		M	F	Y	June	July	Aug.	0500-1100	1100-1700	1700-2300	2300-0500
TL100	S	S	S	S	N	N	S	S	S	S	S
CLASS0	S	N	S	N	N	S	N	N	N	N	N
TL90BS10	S	N	S	0	N	N	S	N	N	N	N
TREMUS	S	N	N	N	N	N	N	N	N	N	N
BS90TL10	A	A	A	A	0	A	N	A	N	N	N
MARMUS	A	N	N	A	N	A	N	N	N	N	N
WILALD	A	A	0	0	0	0	0	0	0	0	0
OTHER @	0	0	0	0	0	0	0	0	0	0	0
BS60TL40	N	N	N	N	0	N	N	N	N	N	N
BS70TL30	N	N	0	0	0	N	0	0	N	0	0
BS80TL20	N	N	N	0	N	N	N	N	N	N	N
TL50BS50	N	N	N	0	0	0	N	0	0	N	N
TL60BS40	N	0	N	N	0	N	N	N	N	N	0
TL70BS30	N	N	N	N	N	N	N	N	N	N	N
TL80BS20	N	0	N	0	0	0	N	N	0	0	0

individual data groupings (table 2). The treed muskeg was similar in vegetation characteristics, although much wetter, to the class-0 habitat. Clumps of tamarack trees scattered throughout this area probably supplied hunting perches. Shrub growth in the treed muskeg was denser (7.35 stems/m²) than in the class-0 habitat but the shrubs were generally associated with clumps of tamarack trees, leaving open areas ideal for hunting. Also, hunting was probably favoured in this habitat due to the presence of both meadow voles and bog lemmings. As was the case in the class-0 habitat, the treed muskeg would provide little cover or concealment for young owls and it is likely that the young tended to remain in the adjacent tamarack bog. The adults probably hunted in the treed muskeg habitat but it was not strongly selected relative to the tamarack bog.

The results of the Bonferroni confidence intervals (table 2) showed that three habitat types were avoided: 90% black spruce-10% tamarack (BS90TL10), marsh-muskeg (MARMUS), and willow-alder (WILALD). Great gray owls were occasionally found in these areas but less than expected according to the availability of that habitat. The remainder of the study area, as described in table 3, was never used by these owls. It was assumed, therefore, that the great gray owls were avoiding these remaining areas since there were no apparent barriers or impediments to their movement into these habitats.

The great gray owls in this study area avoided the 90% black spruce-10% tamarack (BS90TL10) stands and appeared to be neutral towards or avoided any stands that

were greater than 60% black spruce. Of that area never used by the great gray owls, 21% was composed of such stands with more than 60% black spruce (table 3). The avoidance of these stands may be due to the apparently low number of meadow voles available. The majority of species caught in the BS90TL10 habitat were shrews (60%) and no shrews were found in the pellets of the great gray owls in this study. If prey species are not scarce in the study area, then the owls may hunt in those habitats where meadow voles are more abundant.

The marsh-muskeg (MARMUS) habitat was avoided for all data combined and avoided by the young, and in July. Owl use of this habitat in all other cases was not significantly different from the expected use (i.e. not selected or avoided). The marsh-muskeg habitat was a wet habitat with areas of open water. There were no trees growing in this area but clumps of shrubs greater than 2 m in height were scattered throughout. This habitat provided no perches for hunting or resting owls and no cover or concealment. It would have been difficult for pre-fledgling owls to move about in the marsh-muskeg with no trees to climb up or to fly between.

The willow-alder (WILALD) habitat was also avoided overall but in many cases (i.e. for females, young, in June, July and during all time periods except 1100 to 1700) it was not used at all during this study (table 2). Results of the analysis on the use of the willow-alder that did occur showed that the area was avoided by male owls, and by all owls in August. There was no significant difference between

observed use and expected use of this habitat during the 1100 to 1700 (afternoon) time period. This habitat had no trees and the dense shrub growth would have made it difficult for owls to fly through to reach prey on the ground. Again, the lack of trees means no perches or adequate cover for owls.

All other habitat types used by the owls (listed in table 2) were neither selected nor avoided. The remainder of the study area, comprising approximately 620 ha or 32% of the total area, was never used by the owls and was considered to be avoided. Almost 50% of these habitat types that were never used by the great gray owls were composed of stands of black spruce or jack pine (table 3). Avoidance of these black spruce stands was discussed previously. Approximately 33% of this never-used area was composed of stands that were greater than 70% jack pine. Why the great gray owls avoided these habitat types is not certain particularly since meadow voles were available. There may have been a lack of suitable perches in this habitat due to the lack of dead trees and also due to the downward sloping nature of jack pine branches. Young owls would have found it difficult to climb into the jack pine because there were few branches low enough on the trunk and no leaning trees to "walk" up.

Time of day did not appear to affect the owls' selection of habitat. The tamarack bog (TL100) was selected during all times of the day. The black spruce 90%-tamarack 10% (BS90TL10) was avoided in the morning (0500-1100) but was neither avoided nor selected during the rest of the day (table 2). Generally, examining habitat use by time of day did not show any significant patterns of use.

Table 3.--Description of habitats not used by great gray owls.

Major species in habitat (%)	% of area not used
Black spruce 100%	16
Black spruce 60-90%	10
Jack pine 100%	18
Jack pine 70-90%	16
Tr. aspen 50-70%	14
Tamarack 100%	2
Tamarack 60-90%	6
Class-0	7
Unclassified	2
Willow-alder	6
Marsh-muskeg	3
Treed-muskeg	0
Total study area = 1,942 ha	
Never-used area = 620 ha	

Management Implications

Those habitats not used or seldom used by the great gray owls, particularly the black spruce and jack pine stands, should not be dismissed as unimportant to the owls. These avoided habitats, especially the drier stands, could be an important source of prey species. During the relatively dry seasons these prey species may move from these drier areas into the bog and muskeg areas, providing food for the great gray owls. The great gray owls are likely selecting habitat types that can meet most of their biological needs. They would favour those habitats not far from their nest (probably < 1 km), that would provide acceptable prey species, unimpeded hunting (i.e. adequate perches, no dense shrub layer), and cover for shade and concealment from predators for both young and adults.

The results suggest that black spruce and jack pine stands are not critical great gray habitat except as a source of prey species as discussed above. Therefore harvesting these stands which are important to the forestry industry would not seriously affect great gray owl habitat in southeastern Manitoba. If these habitat types are located near (i.e. within 1 km) tamarack bogs or treed muskeg areas, cutting practices could be adjusted to benefit these owls. Cutting these black spruce and jack pine stands would open the canopy allowing for more grass growth and better habitat for small mammal populations. Rather than clear-cutting these areas, trees or patches of trees should be left standing throughout to provide perches for hunting owls.

Stands of black spruce and jack pine without accompanying tamarack bogs or muskeg areas are probably not attractive habitats for great gray owls and could be harvested without serious affect on owl habitat. However, future research would give more insight into the full value of these habitat types. These stands may be used by great gray owls when conditions change. For example, in wetter years when the water level in the tamarack bogs and treed muskeg remains high, prey species, and thus the owls, may move into the black spruce and jack pine habitats. These habitats may also be used more if nests were available. In the study area man-made nests are purposely installed only in tamarack bog habitats. An interesting study could address whether great gray owls would use nests located in adjacent black spruce or jack pine stands.

Great gray owls in southeastern Manitoba appear to select tamarack or tamarack-spruce bogs and treed muskeg areas. Nero (1980) believed that tamarack-black spruce bogs east of Winnipeg are similar in many aspects to owl breeding

range in the northern transition forest. This tamarack-black spruce muskeg area is approximately 40 to 50 km wide and runs about 200 km north and south along the edge of the Precambrian Shield (Nero 1980). This area is composed of old burns, cleared forests, marginal cropland, pine and spruce woods, and bogs and streams. The transitional nature of the forests in this region, a result of burning and clearcutting, possibly makes it prime breeding habitat for great gray owls (Nero 1980).

Although this type of habitat appears to be in sufficient supply in southeastern Manitoba, there is the danger of losing tamarack bog areas to forestry, peat extraction and agriculture. Tamarack forests, once considered to be of marginal value and cut only occasionally for fence posts or firewood, are now being clearcut in extreme southeastern Manitoba as the demand for tamarack for pulp increases (Nero 1984). This practice could leave large areas of the tamarack bog region unsuitable for great gray owl habitation. These bog areas are also threatened by new demands for peat, for mulch in Manitoba and energy in Minnesota, and by continued development of marginal land for agriculture (Nero 1984). Loss of forested boglands means elimination of habitat for owls and other wildlife species (e.g. moose, deer, furbearers). It is important to maintain areas of suitable habitat in southeastern Manitoba where these owls could be available for many people to enjoy.

The status of owls is greatly affected by man's activities and attitudes towards wildlife (Mikkola 1983). Man has an affect on the fate of wildlife populations, directly by destruction of wildlife itself, and indirectly by destruction of habitat. Habitat is probably the single most important factor to consider when attempting to protect a species (Mikkola 1983). Unfortunately little is known about the preferred habitat of the great gray owl across its North American range. There is information only on selected areas such as southeastern Manitoba, central Alberta, northern California and Oregon. We need to know more about the population status of this species across its range, as well as its preferred habitats, so that we are better able to protect those habitats that are critical and able to assess the affects of forestry and other habitat disturbances on the overall population. One of these critical habitats appears to be tamarack

bogs in southeastern Manitoba. A better understanding of the habitat needs of the great gray owl would aid the future management of this species.

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Status of the Great Gray Owl in Finland¹

Olavi Hildén² and Tapio Solonen

Abstract.--The paper summarizes the present information on the occurrence of the Great Grey Owl in Finland, providing a background to a series of colour slides taken by Finnish bird photographers. The number of nests found in Finland has increased considerably since the early 1960s, mainly due to intensified research, but the range and abundance vary greatly from year to year in parallel with the local fluctuations of vole populations. The peak years follow the 3-to-4-year vole cycle. In the latest peak year, 1985, the total Finnish population was estimated roughly at about 1500 breeding pairs. Following aspects are treated in the paper: distribution, abundance and population trends, site tenacity, habitat requirements and the effects of forestry, nest sites, food and hunting technique, movements and invasions.

Up to the middle of the 1960s, the biology of the Great Grey Owl *Strix nebulosa lapponica* in Finland was virtually unknown. But since then, the information has rapidly grown, dozens of nests are found nowadays during peak breeding years, and a number of papers have been published (see the reviews by Hildén & Helo 1981, Mikkola 1981, 1983, Helo 1983, 1984, Solonen 1986). The great interest in this species is shown by the fact that in the vast literature dealing with the ten owl species breeding in Finland, most papers (23%) have been devoted to the Great Grey Owl (Korpimäki 1985).

The aim of this article is to summarize briefly the present knowledge of the status of the Great Grey Owl in Finland, as a background to a series of photographs shown at the symposium. We have focused the presentation on the distribution, abundance and size of the Finnish population, and also given some data on habitats, nest sites and invasions, but largely omitted the breeding biology, food and hunting technique which are described in detail in the recent literature (Hildén & Helo 1981, Mikkola 1981, 1983).

DISTRIBUTION AND ABUNDANCE

In Finland the Great Grey Owl has bred in good vole years in almost all parts of the country, except the northern- and southernmost areas. Because vole populations fluctuate differently in different parts of the country (e.g. Henttonen 1986), also the range and number of Great Grey Owls vary irregularly from year to year (Fig. 1). In most years the breeding is confined to the eastern and relatively northern parts of Finland, but the centre of occurrence varies, and the range seems to have shifted southwards in recent times (Hildén & Helo 1981).

The number of Great Grey Owl nests found in Finland has increased considerably since the middle of the 1960s (Fig. 2), in parallel with the steadily growing interest of bird-watchers in owls. How much the population itself may have increased during this period is hard to say, but Mikkola (1983) and Helo (1984) believe that the species in reality also has become more common. At least a real increase is undisputable compared to the situation from the late 1930s to the early 1960s, from which period very few observations exist (cf. Mikkola & Sulkava 1969, Hildén & Helo 1981). Peak years of breeding have followed at intervals of 3 to 4 years, largely following the annual rhythm of vole cycles.

The most exceptional distribution and abundance of territories was recorded in 1985, when Great Grey Owls bred even on the southern coast of Finland (Solonen 1986). The number of nests and fledged broods found totalled about 70, and at

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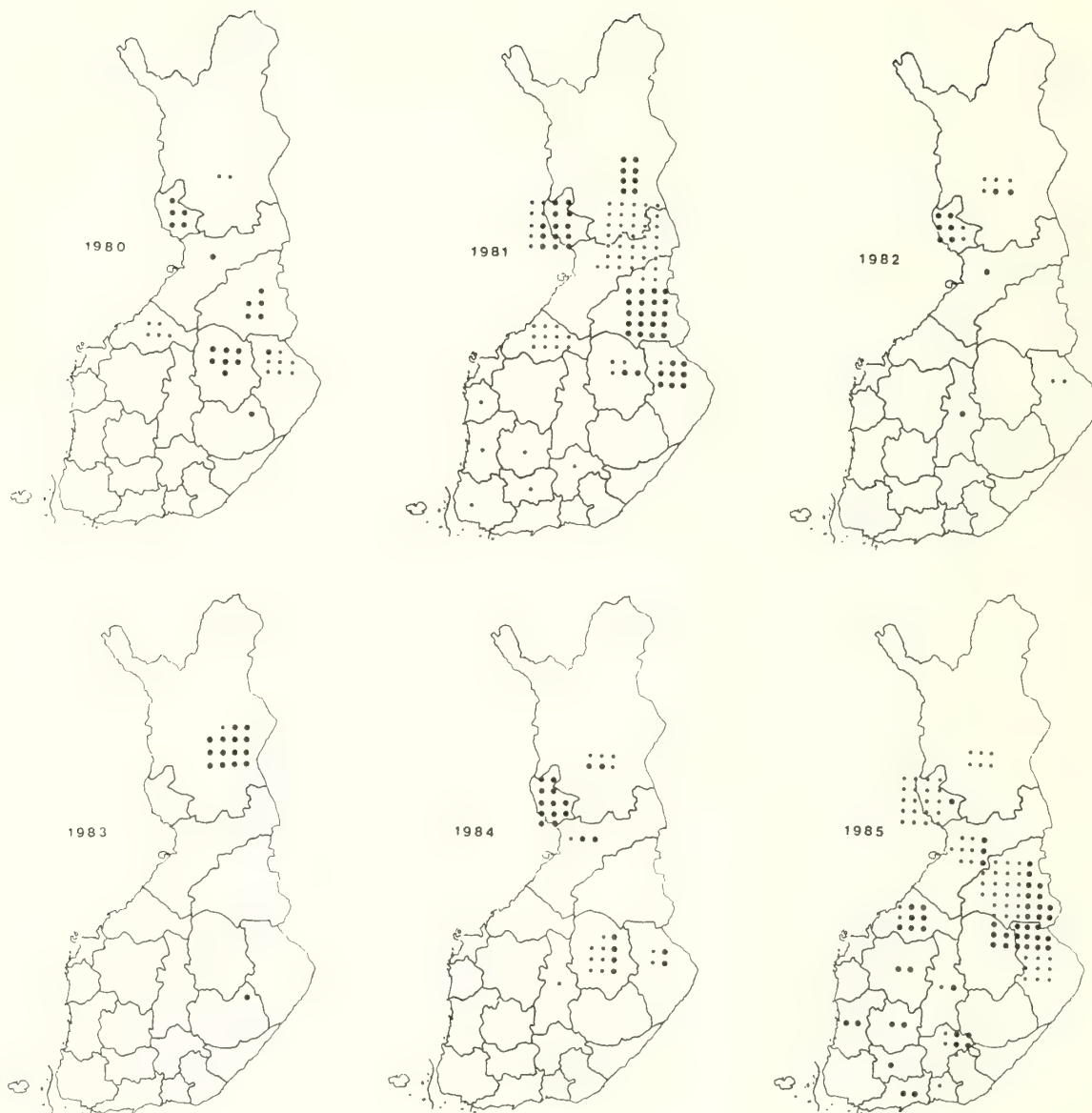
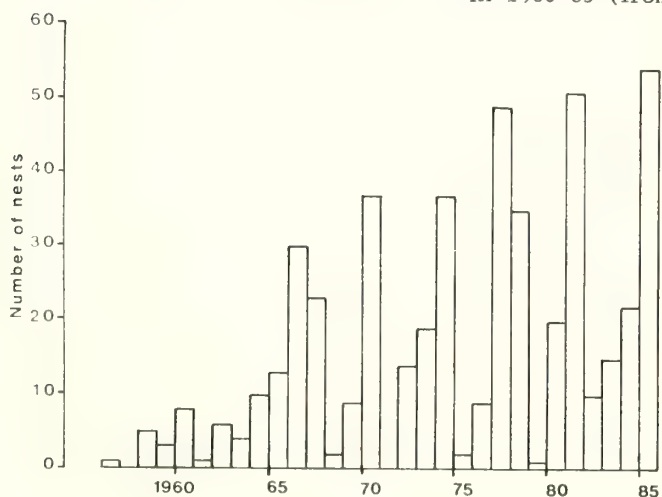


Figure 1.--Territories and nests (large dots) of the Great Grey Owl recorded in Finland in 1980-85 (from Solonen 1986).



least 130 territories were located. The Finnish breeding population was estimated that year at about 1600 pairs (Solonen 1986), based on the approximate number of suitable nest sites (c. 50,000) and the proportion of those occupied by Great Grey Owls in different parts of the country (54 out of c. 3000 checked). This figure is considerably higher than those presented earlier (Saurola 1985), but all the population estimates of this species are inaccurate and should be taken with caution.

Figure 2.--The numbers of Great Grey Owl nests recorded in Finland in 1956-85 (Mikkola 1983, Solonen 1986).



Photo: Antti Leinonen

General densities of the Great Grey Owl are low, but locally there may occur concentrations of several pairs within a few square kilometers. Several occasions of simultaneously occupied nests only 100-300 m apart are known (Hildén & Helo 1981), and in one extreme case the distance was only 49 m (Lehtoranta 1986). At these two nests very close to each other only one male was seen, so polygyny seems possible. Mikkola (1983) has suggested polygyny on two occasions. The breeding concentrations probably are not socially induced but due to an exceptional abundance of voles in certain places and lack of strict territoriality between the pairs (Hildén & Helo 1981).

SITE-TENACITY, HABITAT AND NEST SITES

The Great Grey Owl is a nomadic species, which shifts its breeding areas according to the food situation. Bearing this in mind one can ask, whether it is justified to speak about a separate Finnish population, birds invading Finland from the east in large numbers in certain years and then retiring back again after one or two breeding seasons (Solonen 1986). The species occupies a vast circumpolar range in the northern boreal zone, and it seems to shift the boundaries of its breeding area largely depending on the local vole supply. The abundance of voles both within and

east of Finland probably regulates the movements of the owls in the westernmost parts of the breeding range (Solonen 1987). If the population peak of voles extends over large areas on the Russian side, the nucleus of the species range in Europe, owls need not emigrate to the Finnish side even if there would be a good vole year here. This could explain why Great Grey Owls do not always breed commonly in Finland during mass occurrences of voles. The same holds for invasion birds of the boreal zone in general, e.g. other nomadic owls and crossbills.

How long distances may Great Grey Owls cover when shifting their breeding grounds. Very little is known about this, as the ringing activity has not yet yielded many recoveries. The longest distances recorded so far concern two adult females marked at nest in Norrbotten, Sweden, in 1974 and 1977 and recovered in Finland. The former was controlled breeding in Peokosenniemi, 300 km NE, nine years later in 1983, the latter was found recently dead in Nurmes, 430 km SE, in May 1979. Even much longer movements are quite possible.

Interestingly, the whole population of the Great Grey Owl seems not to be nomadic. Some pairs have been recorded on their territories during poor vole years as well, when they may perform some display and even attempt to nest (Hildén & Helo 1981, Mikkola 1983). Especially on

Swedish side, in Norrbotten, it seems to be a rule that at least some pairs breed, or try to breed, every spring despite poor food supply (e.g. Stefansson 1985, 1986). One could guess that these birds are old, experienced individuals, which are capable of surviving periods of food shortage, at least in years when the crash of voles is not complete. For them, sedentary life may be more advantageous than straggling over long distances in search for better food areas.

The range of breeding habitats accepted by the Great Grey Owl is relatively wide, the two decisive factors being the availability of a suitable nest site and good hunting grounds in the vicinity (Hildén & Helo 1981, Mikkola 1983). The location of the nest may vary from old coniferous forests to clear-felled areas and from uninhabited wilderness to close proximity of houses, and they are almost always situated near open hunting grounds, e.g. marshes, clearings or abandoned fields.

More than 85% of the Finnish nests found were situated in old twig nests of other species, especially those of raptors (Table 1). Because the nests of the most important nest-builders, particularly of the Goshawk *Accipiter gentilis*, are usually situated in old forests, the large-scale destruction of this kind of habitats by modern forestry must be considered a serious threat to the existence of the Great Grey Owl, in addition to many diurnal raptors (Hildén & Helo 1981, Solonen 1986). On the other hand, the species does benefit from clear-cut areas and abandoned fields, which represent optimal habitats for voles and thus provide excellent hunting grounds for the owls. The area of both these man-made habitats has increased considerably in Finland during the last few decades, which at least partly has counterbalanced the contraction of mature forests.

The Great Grey Owl is more versatile in the choice of nest site than most other owl species (Table 1). This gives a good opportunity to man to improve its present nesting possibilities by constructing artificial nests. The experiences obtained so far in Finland are promising: both twig nests built in trees and open boxes filled with sawdust and nailed on stumps have been accepted by Great Grey Owls (e.g. Hildén & Helo 1981). In this way, the species may be attracted to settle in areas providing good hunting terrain but lacking suitable natural nest sites.

The very different nest sites - in raptor nests, on stumps or on flat ground - used by Great Grey Owls are interesting. Is this merely due to an innate versatility of the species nest site selection? Or are there individual differences between birds, e.g. stump-nesting and ground-nesting owls, as believed by Mikkola (1983)? But if so, are these individual preferences genetically determined or do they develop through imprinting, either during the nestling stage or the first breeding? Individual imprinting on a certain nest site type seems the most likely alternative, but the only way to prove

Table 1.--Distribution of nests of the Great Grey Owl by different sites in Finland (Mikkola 1983, Solonen 1986).

Nest sites	N	%
Twig nests of	213	85.5
<i>Accipiter gentilis</i>	102	50.5
<i>Buteo buteo</i>	38	18.8
<i>A. gentilis/B. buteo</i>	16	7.9
<i>Fernis apivorus</i>	7	3.5
<i>Buteo lagopus</i>	6	3.0
<i>Aquila</i> sp.	4	2.0
<i>Pandion haliaetus</i>	1	0.5
<i>Accipiter nisus</i>	1	0.5
Unknown raptor	6	3.0
<i>Corvus corax</i>	6	3.0
<i>Corvus cornix</i>	3	1.5
<i>Pica pica</i>	3	1.5
Man-made artificial stick nests	9	4.5
	202	100
Stump nests	27	10.8
On flat ground	6	2.4
On cliffs	1	0.4
On a large stone	1	0.4
On a barn roof	1	0.4
Total	249	100

this is through intensive ringing of both breeding adults and young, combined with systematic controlling of breeding owls. It is to hope that we after some years will have more data on this problem.

INVASIONS

If food situation remains good, most Great Grey Owls stay within the breeding area or move only short distances. At irregular intervals, however, they perform large-scale invasions far beyond the limits of the breeding range. As in most irruptive birds, they seem to be caused by the combined effect of overpopulation and food shortage. In peak rodent years the owls raise many young, and when the rodent population crashes most birds are faced with starvation unless they leave the area (Hildén & Helo 1981). In such years of exodus, Great Grey Owls invade Finland from the east and may occur locally in astonishing numbers. The two latest invasions, in 1980/81 and 1983/84, are the largest recorded and fairly well documented, although no detailed analysis have been published so far. In 1980/81, hundreds of birds were reported from different parts of Finland, e.g. c. 40 from the district of Porvoo on the south coast and 70-80 northeast of Kajaani in northern Finland (Hildén & Helo 1981). In these two areas with the most abundant occurrence, the owls were spread over 200-300 km², and most of them were seen close to human habitations.



Photo: Seppo Niiranen

Still higher concentrations were observed in winter 1983/84 in the Helsinki district. More than 60 birds were reported here within an area of c. 175 km², about 90% of them east and south-east of the city, especially on some islands where up to seven birds could be seen at the same time (Niiranen & Haapala 1984). That winter the vole population was very scarce in Finland, and probably the owls had been attracted to the Helsinki area by local occurrences of water voles (*Arvicola terrestris*). The food situation was nevertheless so bad that in early March ornithologists began to feed systematically the owls with laboratory mice. Very soon the owls learned to take advantage of the feeding: from afar they recognized the feeder approaching with a plastic pail in his hand, flew to meet him and perched on a nearby branch to wait. As soon as the mouse was put on the snow, the owl swooped down and seized the prey only a few metres from the observers. The boldest individuals even learned to grab the mouse directly from the feeder's hand! More than 200 mice were given to about 25 owls during a month, until the birds gradually disappeared in early April.

In connection with feeding, twenty Great Grey Owls were captured for ringing in Helsinki (Niiranen & Haapala 1984). Surprisingly, 63% of them were more than one year old, and judging from their weight, the majority were females (14 weighed 1000-1280, average 1160 g). This shows that adults also to a large extent participate in invasions, contrary to the irruptive birds in general in which juveniles usually highly predominate (e.g. Hildén 1974). Owls seem to be an exception to this rule, probably because food shortage often is so complete for vole specialists that most adults also are forced to emigrate. In Tengmalm's Owl *Aegolius funereus*, for instance, about 25% of the stragglers ringed in recent years at the Finnish bird stations have been adults, which is not much less than their proportion in the autumn population. For this species, Korpimäki (1981) has shown that adult males are more sedentary than adult females, which is in good accordance to the small sample of Great Grey Owls ringed in Helsinki.

The large-scale emigrations were formerly fatal for Great Grey Owls. Besides those starving

to death, great numbers of owls were shot, as shown by the statistics of birds sent to taxidermists and museums (cf. v. Haartman et al. 1963-72, Mikkola 1983, p. 209). Fortunately, the attitudes towards owls and raptors have totally changed, both in Finland and most other countries. A good example of this was the successful feeding operation of Great Grey Owls in Helsinki, as well as the positive publicity these magnificent birds gained in mass-media all over the country.

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Territorial Aspects of Barred Owl Home Range and Behavior in Minnesota¹

Thomas H. Nicholls² and Mark R. Fuller³

Abstract.--We described the movements of barred owls (*Strix varia*) based on samples taken from millions of telemetry data recorded by a semi-automatic radio-tracking system. Evidence collected convinces us that barred owls are territorial in habit. They exhibited nearly exclusive use of their home ranges within their own species. When home ranges of neighboring owls did overlap, it was of short duration and consisted of a small portion of the total home range. However, home ranges of mated pairs overlapped extensively. Home range boundaries were generally constant from year to year and decade to decade, even when occupants changed. Neighbors were seldom near each other. Vocal advertisement was apparently the most important display. The few barred owls that did not exhibit territoriality were thought to be young, or dispersing birds.

INTRODUCTION

Territoriality in birds and animals has been addressed by many authors who have variously defined the term and recommended different criteria for determining territories and territorial behavior. The most commonly accepted definition of a territory is: A fixed area that varies little through time, from which rivals are excluded, and in which the occupant conducts some or all of its activities (Brown 1975, Morse 1980, Mittenberger 1981).

Given this definition, several workers have reported territorial behavior by various species of owl: great horned owl, *Bubo virginianus* (Miller 1930, Baumgartner 1939); flammulated screech owl, *Otus flammeolus* (Marshall 1939); snowy owl, *Nyctea scandiaca*, (Keith 1964, Evans 1980); and tawny owl, *Strix aluco* (Southern 1970, Southern and Lowe 1968). To further support the concept of territoriality among owls, we present

the results of our studies on the home ranges and movement patterns of the barred owl, *S. varia*. (We define "home range" as that area regularly used by an owl during its normal activities of hunting, courtship and mating, nesting, caring for young, and seeking shelter.) We conducted our two studies on the Cedar Creek Natural History Area (CCNHA) in Minnesota. We used radio telemetry to track the birds. This permitted short sampling intervals, useful for evaluating the short-duration activities of owls necessary to describe territoriality.

METHODS

The CCNHA, a 5,460-acre research facility operated by the University of Minnesota, is located at 93° 12'E longitude and 45° 24'N latitude about 30 miles north of Minneapolis, Minnesota. The area contains a blend of forests, prairies, marshes, lakes, ponds, and abandoned fields of various ages (Pierce 1954, Bray et al. 1959). Nicholls and Warner (1972) described the general seasonal and phenological characteristics related to barred owl habitat use.

Owls were trapped using balchatri traps, Swedish goshawk traps, and two-shelf mist nets (Nicholls 1973, Fuller and Christenson 1976). Owls were measured, sexed when possible, fitted with radio transmitters (Nicholls and Warner 1968, Fuller 1979), banded, and released (fig. 1). We concluded that birds were a pair if they cared for the same young owls during the breeding season.

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Figure 1. A barred owl equipped with a radio transmitter completely covered by feathers.

The owls were tracked by a semi-automatic radio-tracking system developed by Cochran et al. (1965). The system consisted of two rotating directional receiving antennas on towers about half a mile apart. Each owl's transmitter operated at a different frequency. Signals were received at a central laboratory every 45 seconds, providing a maximum of 1,920 daily locations determined by azimuth triangulation. Received signals were recorded on film and transcribed to computer tape for data analyses.

Nicholls (1973) radio-tracked 10 barred owls during 1965 and 1966, sampling more than 28,000 owl locations from more than two million locations recorded. The sampling interval was normally every 15 minutes at night and every 30 minutes during the day. Fuller (1979) radio-tracked four barred owls from 1971 to 1973, sampling every minute every-other-day, and every 15 minutes on the alternate days. In both studies, locations sampled while an owl was in flight were not used because such location data are subject to error.

Home range was determined by overlaying the study area map with a grid of 2,080, 1.6-acre squares. Square size was based on error factors that influence the accuracy of location data obtained by the triangulation method (Fuller 1979). Squares were numbered for computer identification. Using degree bearings obtained from the two radio tracking towers, a computer program assigned each location to a 1.6-acre square. Proximity of birds was based on the number of grid squares (about 264 ft on a side) separating their locations.

Nicholls (1973) determined home range size by summing the total number of squares within the home range boundary delineated by the outermost 1.6-acre squares with owl locations in them (fig. 2). Those few squares without owl locations but inside home range boundaries were considered part of the home range. Fuller (1979) used a similar method, the "grid square plus fill" method (Rongstad and Tester 1969) that was also based on the 1.6-acre grid system. When the computer scanned across the grid, it included squares in the home range even if they did not contain locations when they were between locations separated by not more than five squares along either the vertical or horizontal axis. These methods include a conservative number of squares that an owl might have utilized or flown over.

Useful home range data were obtained for 13 of 17 barred owls radio-tracked (table 1). The home ranges of nine barred owls that Nicholls (1973) radio-tracked from 7 to 28 weeks ranged from 213 to 912 acres. The home ranges of four owls that Fuller (1979) studied from 3 to 30 weeks ranged from 309 to 1,903 acres. The average home range size for these 13 owls was 676 acres based upon 249,623 owl locations.

RESULTS AND DISCUSSION

Overlap of adjacent owls' home ranges

We found four cases of neighboring owls not sharing any parts of their home range during radio-tracking and several examples of brief and limited use of common area by neighbors (table 2). Historically, the exclusive or nearly exclusive use of space, has been a key element of the territory concept (Brown 1975, Wittenberger 1981). No home range overlap was detected among three barred owls tracked in 1965 (fig. 3) or among two owls studied in 1972 (fig. 4). Spatial patterns alone are not evidence of territorial behavior, but territorial behavior tolerates little or no overlap of home ranges (Brown 1975).

Simultaneous radio-tracking of barred owl 709, 710, and 714 revealed limited overlap of their home ranges (fig. 5). Owl 709 spent over 98 percent of its time north of the county road and 714 spent all of its time south of the county road. There were only 11 acres of overlap between the adjacent home ranges of male 710 and male 714 and only 3 acres of overlap between owl 709 and male 710 (table 2 and fig. 5). Some authors maintain that the exclusive use of an area is required for it to be considered a territory, but Brown (1975) claims the important thing is that intruders are driven from a territory when encountered. If a home range includes limited resources (e.g. food, nest site, shelter), neighbors will sometimes enter another's territory.

How often and how long owls share a territory is revealed in another example. An intensive sample of locations from non-breeding female 730

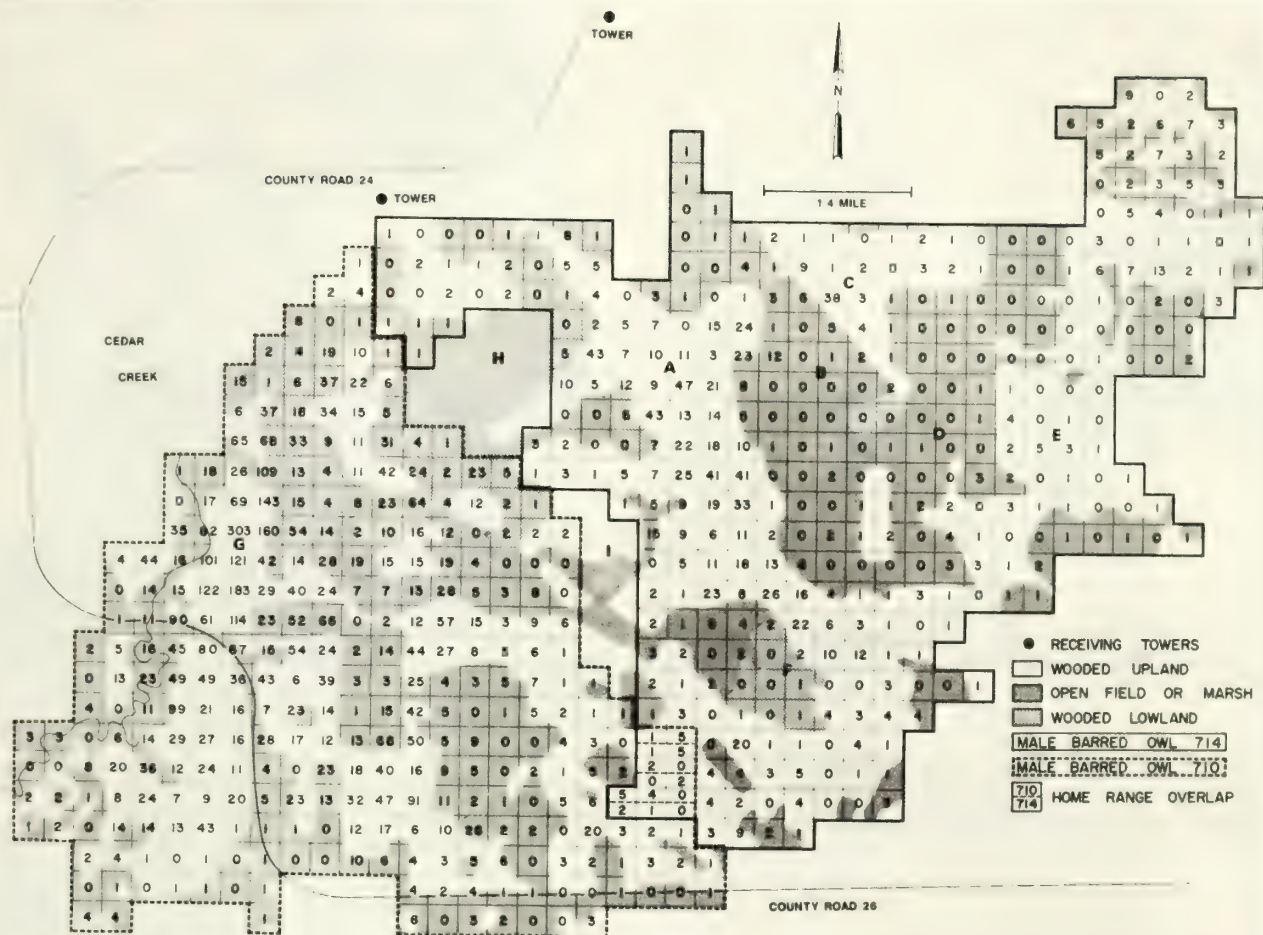


Figure 2. The 502-acre home range of male 710 from March 10 to September 11, 1966, and the 611-acre home range of male 714 from March 22 to October 4, 1966, on the Cedar Creek Natural History Area. Each square is 1.6 acres; numbers in squares indicate the number of radio locations. Note territorial boundary and 11-acre home range overlap where territorial displays were observed.

in 1973 showed parts of her weekly home ranges were interspersed with those of a breeding pair. She was detected in one or more of the same grid squares that were used by male 731 in 12 of 14 weeks of simultaneous radio-tracking, but these two owls were never detected closer than 1,319 ft to each other. However, non-breeding female 730 did range near the mate of 731, breeding female 720b. The closest they were detected was 528-791 ft for 6 minutes. They were also recorded within 1,319 ft of each other over a 4-week period for 82 minutes. The total time spent within 1,319 ft of each other totaled 0.01% of the 4 weekly periods when proximity was detected. These two females shared 1.5 - 7.9 acres (average 4.2 acres) in 10 of 14 weeks. This shared area included 1.4 - 68.0% of the weekly home range of the breeding owl and 0.7 - 5.8% of the weekly area used by the non-breeding bird.

Thus, our evidence suggests that individuals spend at most only a small percentage of their time within the range or in proximity to neighbors. Trapping results, positions of owl vocalizations, and observations of owls led us to assume that no other owls (except mates) established home ranges in the areas used by the radio-marked birds. A few examples of movements by owls that did not establish home ranges (documented in the Non-territorial birds section) also support this assumption.

Home range overlap of mated owls

We found extensive overlap between members of the two barred owl pairs we radio-tracked. Female 702 and her mate, male 714, were trapped in the same mist net in March 1966. During the next 2

Table 1.--Home Ranges of barred owls on the Cedar Creek Natural History Area, Minnesota.

Barred ¹ Owl	Home Range (Acres)	No. Owl Locations	Period Radio-Tracked
701	213	2,132	5/19/65 - 8/9/65
702	515	943	3/22/66 - 5/19/66
703	258	2,479	7/15/65 - 9/20/65
704	768	4,746	11/12/65 - 2/13/66
707	809	1,705	2/15/66 - 8/15/66
709	912	5,959	2/23/66 - 9/11/66
710	502	5,043	3/8/66 - 9/11/66
712	493	2,213	3/14/66 - 5/5/66
714	611	1,345	3/22/66 - 10/4/66
717b	309	40,148	5/25/72 - 8/3/72
720a	901	18,085	6/29/72 - 8/31/72
720b	474	43,878	3/8/73 - 6/7/73
730	1,903	86,830	2/27/73 - 9/4/73
731	793	34,117	3/7/73 - 6/6/73

TOTALS
13 \bar{X} = 676 249,623

¹Owls radio-tracked by Nicholls (1973) = 701 to 714
Owls radio-tracked by Fuller (1979) = 717b to 731

Table 2.-- Some home range relationships of barred owls on the Cedar Creek Natural History Area, Minnesota, during 1965 and 1966.
(F = Female, M = Male)

Owl Number	Number acres overlap between home ranges	Radio- tracked at same time	Comments
701F 703	0	Yes	701 occupied home range south of 703
709 710M	3	Yes	710 occupied home range south of 709
702F 710M	3	Yes	710 occupied home range west of 702
714M 710M	11	Yes	710 occupied home range west of 714
704M 710M	16	No	710 occupied home range west of 704
709 702F	102	Yes	709 occupied home range northwest of 702
709 714M	136	Yes	709 occupied home range northwest of 714
701F 710M	199	No	701 was suspected mate of 710
702F 704M	449	No	704 was suspected mate of 702 before he died
702F 714M	467	Yes	702 and 714 were paired
714M 704M	558	No	714 took over 704's home range after he died

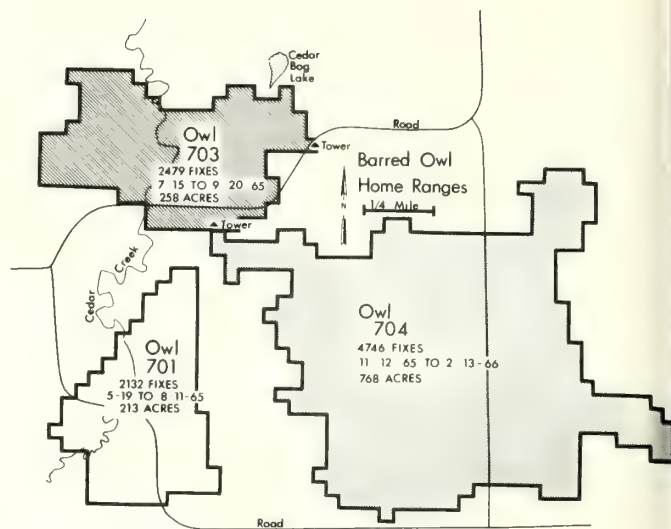


Figure 3. The geographical locations of home ranges occupied by female 701, 703 (sex unknown), and male 704, mostly studied in 1965, were territorial and showed no overlap in their home ranges.

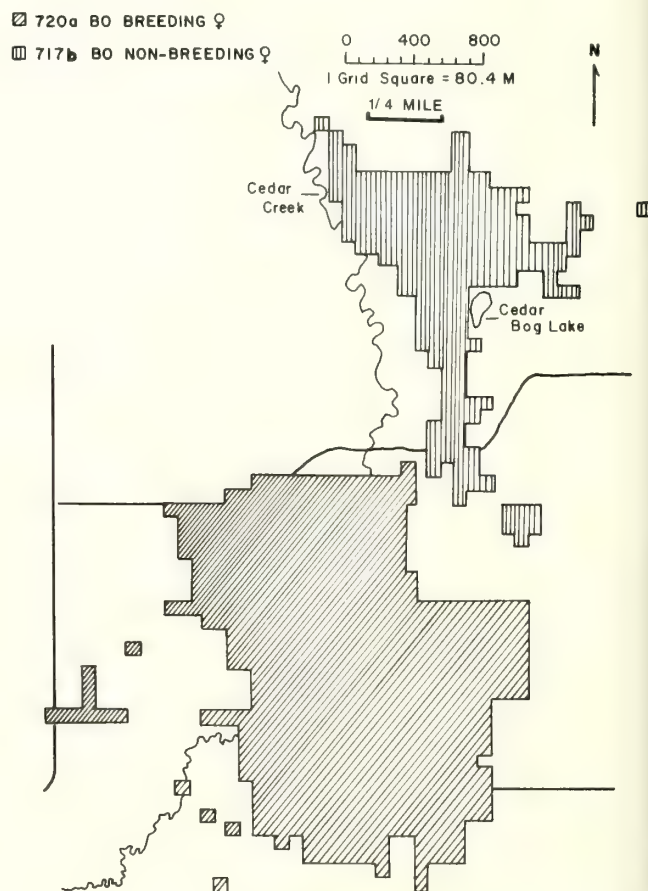


Figure 4. Non-breeding female owl 717b (studied from May 25 to August 3, 1972) and breeding female 720a (studied from June 29 to August 31, 1972) were territorial and showed no overlap in their home ranges.

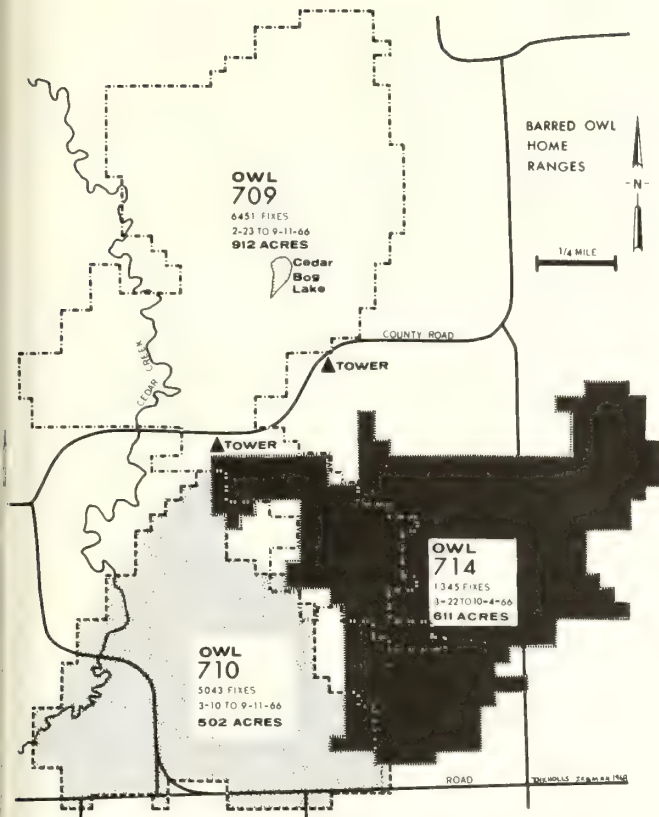


Figure 5. Home ranges of barred owl 709, male 710, and male 714 showed that all three owls had little overlap of their home ranges. The small overlap of 709's home range into 714's was a result of a few brief trips into 714's home range. Vocal territorial displays were documented in the overlap area.

months, 87% of the female's total range (449 of 515 acres) was within the area used by her mate (fig. 6a). Similarly, more than 95% of the range of female 720b was shared with her mate, 731, from March to June in 1973 (fig. 6b). Females of many monogamous species do defend territories (Morse 1980). Southern (1970) found that female tawny owls joined their mates in displays at territory boundaries. An energy-efficient strategy for two birds would be to defend the same boundary, within which there were just enough resources to support both of them (Brown 1975). The size of the territory depends mainly on the type(s) of resources to be defended and the ultimate factors influencing the behavior (Wittenberger 1981).

Persistence of boundaries

Our maps of radio-locations showed that home range positions on the study area remained similar during 2 consecutive decades. Barred owls do not use all of their home range each night, or each week, but after several weeks, the core areas are re-used and few boundary changes occur (Nicholls 1973, Fuller 1979). Barred owl areas of use thus meet the fixity criterion for territoriality (Brown 1975).

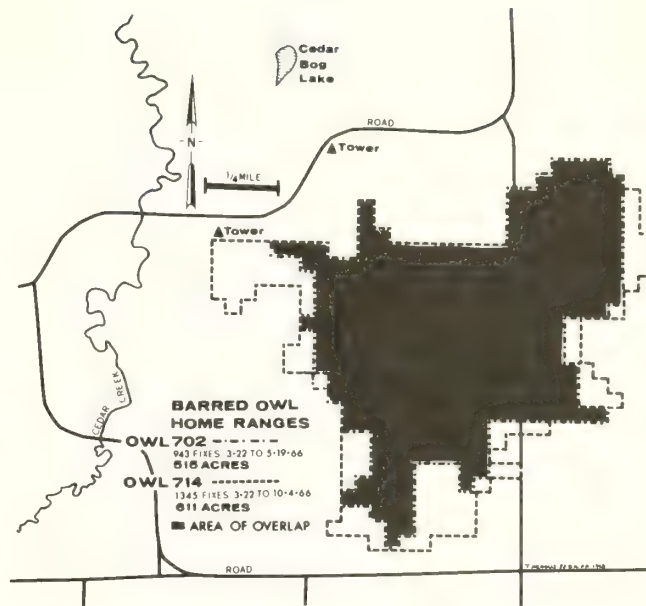


Figure 6a. Overlapping home ranges of a pair of barred owls, female 702 and male 714, during 1966.

- 720b BO BREEDING ♀
- 731 BO BREEDING ♂
- = Nest

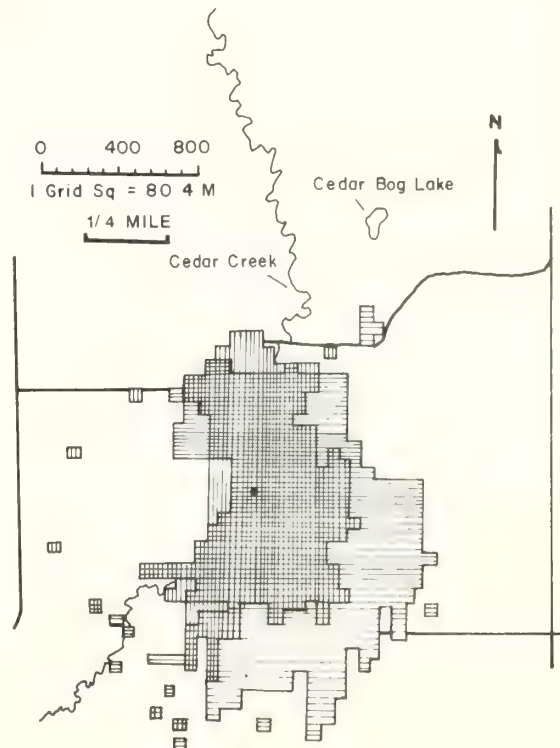


Figure 6b. Overlapping home ranges of a pair of barred owls, female 720b and male 731, during 1973.

We had two cases in which a female owl (720 and 702) used much of the same area in consecutive years (figs. 4 and 6a). Even when a new bird replaced a previous occupant, home range boundaries remained similar. For example, male barred owl 704 died and was replaced by male 714. During the next 6 months, 72% of 714's range was the same area used by 704 (figs. 3 and 5). Similarly, from December 1971 to August 1972, female 717 occupied the area north of the county road then, after the disappearance of 717, female 730 was radio-tracked in that area from February through August 1973.

Comparing maps from the 1960's with those from the 1970's shows that similar boundaries persisted from one decade to the next. In the 1970's, barred owls also did occupy the area used by 704 and 714, but they were not radio-tracked. Southern (1970) documented constancy of tawny owl boundaries for 13 years, and noted that for long-lived birds (e.g. survival of > 4 years for individuals surviving to maturity), territory boundaries probably remain fairly constant, assuming resource distribution does not change appreciably. It is unlikely both members of a pair, or neighbors, die at the same time, thus, one territory holder will remain to maintain the boundary.

Vocalizations related to territoriality

Our experience suggested that owls vocally communicate with their mates, delineate their territory, and signal its occupancy. Vocalizations often advertise the presence of territorial birds (Wittenberger 1981). Baumgartner (1939) reported great horned owls making a circuit, associated with calling, around their "domains." We often heard two to four barred owls calling in sequence. These calls came from locations that formed a pattern similar to the pattern of home ranges based on telemetry. The calling from within home ranges, in conjunction with a few documented instances of vocal displays at home range boundaries, is additional evidence of territorial behavior. Southern (1970) obtained similar results with tawny owls.

The first boundary encounter involved two barred owls that were heard hooting about 0.8 mi apart at 1400 hours on, March 4, 1966 in the vicinity of the boundary between the the home ranges of owls 710, 702 and 714 (fig. 2). The hooting continued and the owls perched closer and closer until they sounded to be within about 15 yards of one another. Hooting became frequent, and loud calls, similar to those reported by Bent (1938), were heard. After about 10 minutes, the owls retreated toward the center of their ranges. Hooting was heard later from the positions where the owls were initially detected.

Another bout of vocalization occurred in the same vicinity at 0910 hours on March 21, 1966. The owls were already within a few yards of each

other and calling several times a minute. There were frequent flights back and forth, but there was no indication that the birds made physical contact. The positions of the calls suggested a chase and retreat behavior. After 20 minutes all hooting stopped. The home range maps of male owls 710 and 714 revealed a definite boundary with only an 11-acre overlap in the area where the vocalizations were heard (fig. 2).

Evidence of expulsion of an intruder was gathered between 1930 and 2200 hours on April 28, 1966. Loud caterwauling, as described in Bent (1938), was heard; radio-telemetry data suggested the birds doing the hooting were paired owls 702 and 714 (fig. 6a). Subsequently, a third owl, 709 (fig. 5), was heard nearby and the first two flew toward the newcomer. It quickly retreated and the interaction ended. After this encounter, owl 709 did not enter the range of owls 702 and 714 for at least 20 days. Then, between May 19 and June 8 it made two brief trips into their range. From June 8 until September 11, 1966, owl 709 never reentered the area used by 702 and 714.

A tape recording of barred owl calls was played within the territory of 702 and 714 on May 4, 1966 at 2200 hours to see if the pair would respond to another owl within their territory. Within 12 minutes both owls responded by hooting, flying toward the tape recorder, and landing in trees overhead. Human imitations of a barred owl hoot elicited a response from owl 710 in his nest area on several occasions. Subsequently, broadcasts and human imitations of barred owl vocalizations have been used to attract owls to mist nets for capture and radio-marking on the CCNHA (Kuechle et al. in press), and barred owl calls have been used to elicit responses for surveys (Fuller and Mosher 1981, McGarigal and Fraser 1985). Miller (1930) imitated great horned owl vocalizations and attracted owls to boundaries but could not induce them to cross into a neighbor's range. Vocalizations and sometimes chasing are apparently the ways barred owls establish and defend their territories.

Non-territorial birds

Some barred owls did not exhibit territorial behavior. These birds were thought to be young or dispersing birds that moved into the study area and could not successfully establish territories. For example, owl 729 was radio-tracked from January to April, 1973, and used the area along the eastern edge of the range of 730, the north and east edges of the ranges of pair 720-731, and the area east of this pair's range that was used by unmarked barred owls. In April, 729 moved to the northeast and eventually out of the study area. Owl 712 also left the area after being radio-tracked for 52 days from March 14 to May 17, 1966. This behavior suggests resident holders enforce a degree of exclusive use of certain areas within their established home ranges and that there are "homeless" owls searching for an area to settle in. Settling behavior was documented for

tawny owls by Southern (1970); other observations and experiments with territorial species have demonstrated the existence of "floaters," waiting to establish territories (Davies 1978).

CONCLUSION

Our studies revealed that barred owls maintain nearly exclusive home ranges, expel intruders and neighbors from their ranges, and vocalize to advertise the occupancy of their space. These behaviors are consistent with criteria for territoriality. Territorial behavior that leads to nearly exclusive use of space has a variety of advantages for occupants (Brown 1975). Apparently, nearly all the barred owls' activities occurred in their territories, which corresponded with their home ranges. This relationship is the Type A territory of Hinde (1956).

Hinde discussed many potential advantages for territory holders: protection of nest and nest site, prevention of epidemics, reduction of loss to predation for cryptic species, prevention of inbreeding, facilitation of pair formation and maintenance, prevention of interference with reproductive activities, and exclusive use of limited resources, including short-term requirements of the occupant (e.g. food for young). Being territorial, the barred owl benefits from many of these advantages.

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Barred Owls and Nest Boxes — Results of a Five-Year Study in Minnesota¹

David H. Johnson²

Abstract. Thirty-six nest boxes were monitored 5 years to evaluate Barred Owl (*Strix varia*) nesting biology, habitat characteristics, and box design and placement. Boxes were erected in 1981 and 1982, and were placed at least 1.6 km apart in various forest habitats. Fourteen boxes used by owls for 1-3 seasons produced 22 nestings (12.4% overall nest box use), with 86% of nesting attempts successful. Predominant nesting use occurred in the northern hardwood forest type. Habitat evaluation surrounding the 14 active boxes and 10 additional nest sites (8 natural cavities, 2 nest boxes) included 0.04 ha and 314 ha circular plots. Recommendations include using a topless nest box or one with a side entrance hole of \geq 18 cm diameter. Box placement should avoid raccoon (*Procyon lotor*) travelways, be 7 m above ground, and allow easy in-flight access.

INTRODUCTION

The Barred Owl is a close relative of the European Tawny Owl (*S. aluco*) and Ural Owl (*S. uralensis*), and the North American Spotted Owl (*S. occidentalis*). As such, some similar natural history characteristics should apply between these species. Like Tawny and Ural owls, Barred Owls have been found to nest in artificial nest cavities (Rubey 1927, Johnson 1980, Snyder and Drazkowski 1981, Follen 1982, Johnson and Follen 1984). The availability of suitable nest sites is reported to be a limiting factor for cavity nesting species (Thomas et al. 1979). Current forest management directives promote short rotations and intensive culture, which reduce the numbers of existing or potential nest sites. The Barred Owl is a relatively common owl in Minnesota, and has recently been viewed as an ecological indicator species for the management of mature/old

growth forests. This study was conducted as part of an overall research effort into Barred Owl ecology in the state. Herein I provide information on nest boxes, their use by owls and other wildlife, and an overview of habitat conditions surrounding used nest sites.

STUDY AREA AND METHODS

The study area involved Hubbard, Becker, Cass, and Crow Wing counties in north-central Minnesota (1,336,600 ha). This area lies primarily at 47 degrees North latitude, averages 64 cm of precipitation annually, and has a 125 day growing season. Snow covers the ground an average of 130 days per winter. The terrain is typically level to slightly rolling. Water is relatively abundant with around 2000 lakes and rivers totaling approximately 200,000 ha (15% total land area). Forests in this region cover some 796,000 ha (60% total land area) (Jakes 1980) and consist primarily of 50 to 80 year old mixed and pure stands of aspen (*Populus* spp.), oak (*Quercus* spp.), maple (*Acer* spp.), basswood (*Tilia americana*), paper birch (*Betula papyrifera*), elm (*Ulmus* spp.), black ash (*Fraxinus nigra*), and jack pine (*Pinus banksiana*). Widespread logging and slash burning during the late 1800's and

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early 1900's has resulted in an even-aged forest in which natural cavities are scarce. The predominant land use is logging, followed by agriculture (dairy, corn, wheat, potatoes) and tourism.

Boxes were placed in what was viewed as potentially suitable owl habitat, based on the literature and experience. Pre-placement surveys were not conducted. Boxes were of two types: a covered box with an entrance hole of approximately 18 cm diameter ($n = 34$) or a topless box ($n = 2$). All were made of 2 cm thick unpainted/untreated wood and measured roughly 29 x 26 x 55 cm (inside length x width x depth). All boxes were placed from 4.11-10.87 m ($\bar{x} = 6.14$ m) above ground on living trees 16.5-63.5 cm dbh ($\bar{x} = 37.1$ cm), and were mounted with either the back ($n = 8$) or a side of the box ($n = 28$) immediately adjacent to the tree trunk/branch. See Johnson and Follen (1984) for box design and mounting details. Twenty-eight (28) boxes were placed on deciduous trees and 8 boxes on coniferous trees. Entrance hole orientation depended on anticipated owl flight access. Approximately 5 cm of small wood chips or leaf material was maintained in the boxes as nesting substrate.

Boxes were erected prior to the breeding seasons of 1981 or 1982. Three or more inspections were made yearly; the first during early January (done primarily to clean out leaf material put in the preceeding fall by dispersing squirrels), the second and third done in early April and mid-May respectively, to check for nesting activity. Additional checks were made if owls were nesting. Climbing irons, belt, and rope were used throughout the project to scale the trees.

Nest site habitat data were collected at 24 separate Barred Owl nest sites during the leaf-free season following the first nesting use. These sites included 14 of my nest boxes, 2 other nest boxes, and 8 natural cavities. Two types of circular plots were employed: a 0.04 ha (11.3 m radius) plot and a 314 ha (1 km radius) plot. Both were centered on the nest tree. Table 2 lists 15 quantitative habitat variables that were either measured directly or created by aggregate at the 0.04 ha plots. Sampling procedures were similar to those as described in James and Shugart (1970) and Titus and Mosher (1981). Habitat evaluation also included recording the nest tree species, box mounting style, entrance hole compass orientation, and forest type within 100 m of the nest site.

Seven (7) habitat types were measured at the 314 ha plots: forest, water, upland brush/upland and lowland grass, marsh, agricultural fields, lowland brush, and roads. Types were interpreted to the nearest 0.4 ha from 1:15,840 black and white infra-red aerial photos, copied onto frosted matex overlays, and hectarized via a dot grid.

RESULTS

Box Use by Owls

Fourteen (14) boxes (12 covered and 2 topless) were used by owls for nesting a total of 22 times (12.4% overall nest box use). An additional 4 boxes were recorded as having owl visitation. Seven (7) boxes were used only once for nesting, 6 boxes two times, and 1 box three times (Table 1). Nineteen of 22 nests (86%) were successful in raising young to or beyond the "brancher" stage (i.e. 25-30 days old). At the 19 successful nests, 52 eggs (2.73/clutch, range 2-4) produced 46 young (2.42/nest, range 1-4). Three (3) nests were predated by raccoons, 2 at the egg stage (box 25, 1983 and 1984), and 1 with approximately 15 day-old young (box 21). I feel that I was the cause of predation at the two nests lost at the egg stage (raccoons followed scent trail). No re-nesting attempts were made at any of the unsuccessful nests.

Table 1. Barred Owl nesting activity in boxes.

Box#	1981	1982	1983	1984	1985	1986
1	4/4*	2/1	-	-	-	-
43	3/3	-	-	2/2	-	-
44	3/3	-	-	-	-	-
3	4/3	-	-	-	-	-
8	-	2/2	2/2	-	-	-
15	-	3/3	-	-	-	-
19	-	-	3/3	3/2	-	-
21	-	-	3/0	-	-	-
22	-	-	-	3/3	-	-
25	-	-	2/0	2/0	2/2	-
33	-	-	2/2	-	-	-
34	-	2/2	-	-	-	3/3
36	-	-	-	-	-	3/2
45**	-	-	3/2	3/2	-	-

* number of eggs laid/number of yng. raised.

** box #45 was available for use only 4 years

As indicated in Table 1, owl nesting activity in the boxes was rather staggered. Although no detailed records were kept, pairs were often seen on their territories during the non-nesting years (via territorial responses to taped calls and observations of delayed courtship

activities). It is my opinion that the sporadic nesting recorded was the result of fluctuating food sources, rather than the undocumented use of alternate (and unknown) nest sites.

It is of interest to note that at one box, occupancy by owls was relatively quick after box placement. Box 45 was erected on 04-02-83 and owls had eggs in it by 04-09-83.

During fall dispersal, squirrels often placed 25-30 cm of leaf and twig material into the boxes. In 2 instances, owl visitation (but no nesting) was noted when this deep, rather loose leaf matter was in the box.

In a third case the owls did appear to compact and nest on this leaf material.

Four boxes were placed within 100 m of four pre-existing nest sites, to offer an alternate nest site. Boxes 1 and 3 were placed near natural cavities, 30 and 36 were placed near topless wood duck boxes. In three of the four cases, owls

moved into the box I provided; details as follows. The natural cavity near box 1 was a 2 m vertical trunk split in a live basswood tree. The tree cavity was deteriorating and although the birds nested there in 1977 and 1978 they did not use it thereafter. In 1981 and 1982 nesting at this site occurred in box 1.

The natural cavity near box 3 was a hollow branch stub in a live basswood tree. This nest site began when a 23 cm branch was cut off in 1965, subsequent callus growth and interior rot developed the nest cavity. Wood ducks (*Aix sponsa*) nested here 1975-1979, and owls in 1980. The owls used nest box 3 in 1981. Owls with young were heard for an extended period approximately 300 m from the box in 1983, and likely reflect the nesting use of a third (but unlocated) nest site.

The topless wood duck box near box 30 was used for nesting in 1980, 1981, and 1984. Although it was not used for nesting, owl visitation was recorded for box 30.

The topless wood duck box near box 36 was used for nesting only in 1980 and 1981. In 1986 owls nested in box 36.

Table 2. Description of quantitative habitat variables measured at 22 Barred Owl nest sites.

Mnemonic	Description
1. HTNSTTRE	height of nest tree in meters
2. DBH	diameter at breast height of nest tree in cm
3. CAVHT	above ground height of cavity in meters
4. CANHT	average height in meters of canopy in or adjacent to plot
5. NTAGE	age of nest tree in years
6. CANAGE	average age of canopy trees in or adjacent to plot
7. NOTREES	number of all trees > 5 cm dbh and > 2 meters tall per ha
8. DBHLT25	number of all trees 5-25 cm dbh and > 2 meters tall per ha
9. DBH2648	number of all trees 26-48 cm dbh and > 2 meters tall per ha
10. DBHGT48	number of all trees > 48 cm dbh and > 2 meters tall per ha
11. LVEVER	number of live evergreen trees on plot > 5 cm dbh and > 2 meters tall per ha
12. PERSLOP	percentage slope of plot
13. HUMHAB	distance in meters to nearest human habitation
14. WATER	distance in meters to nearest early season water (stream, river, pond, lake)
15. FOROP	distance in meters to nearest forest opening; measured to the nearest upland break in the forest continuity, such as created by a trail, field, etc.

Habitat Evaluation

Five (5) back-mounted and 9 side-mounted boxes were used. Compass orientation of entrance holes from 12 used boxes and 6 natural cavities were pooled and placed into 8 quadrants for evaluation (i.e. quadrant A = 1-45 degrees, quadrant B = 46-90 degrees, and so on). Quadrants A, B, C, D, E, F, G, and H held 5, 0, 2, 2, 2, 1, 4, and 2 nests respectively. No significant difference was found in regards to entrance hole orientation (chi-square = 2.389). Entrance holes for 4 additional nests faced skyward and thus were not included in the above evaluation.

Heights of 14 used nest boxes were compared to 22 unused boxes and 7 natural cavities using T-tests. Although heights for used boxes (\bar{x} = 6.2 m, range 4.1-10.9 m) differed little from unused boxes (\bar{x} = 6.1 m, range 4.7-7.6 m), P = 0.90, they did differ from natural cavities (\bar{x} = 8.2 m, range 6.3-11.0 m) P = 0.034.

Tree species on which used boxes were located include: red oak (*Q. rubra*) (n = 4), bur oak (*Q. macrocarpa*) (n = 1), basswood (n = 2), white elm (*U. americana*) (n = 2), red elm (*U. rubra*) (n = 1), black ash (n = 2), jack pine (n = 1), red pine (*P. resinosa*) (n = 1), and white pine (*P. strobus*) (n = 1). Natural

Table 3. Means, standard deviations, and ranges of habitat variables for 22 Barred Owl nests.

variable	\bar{x}	SD	range
HTNSTTRE	17.2	3.8	9.1-25.0
DBH	43.4	15.5	16.5-80.5
CAVHT	6.7	2.1	3.4-11.0
CANHT	17.8	3.2	12.8-25.0
NTAGE	91.7	39.1	47-200
CANAGE	65.1	15.1	36-96
NOTREES	670.5	302.2	100.0-1150.0
DBHLT25	536.4	281.9	75.0-975.0
DBH2648	119.3	60.2	0.0-250.0
DBHGT48	14.8	16.7	0.0-50.0
LVEVER	34.1	68.0	0.0-300.0
PERSLOP	6.5	5.9	0.0-20.0
HUMHAB	762.0	840.7	12.5-2667.0
WATER	122.3	189.5	0.0-612.6
FOROP	47.3	55.2	0.0-198.1

Table 4. Forest types within 100 m of 24 Barred Owl nests.

forest type	#nests	%
northern hardwoods	15*	62.5
lowland hardwoods	4**	16.7
aspen/birch	3	12.5
oak	1	4.2
jack pine	1	4.2

* includes 6 natural cavity nests

** includes 2 natural cavity nests

Table 5. Habitat characteristics within a 314 ha (1 km radius) circular plot at 24 Barred Owl nests.

habitat	\bar{x} ha	SD	range	%
forest	211.0	47.9	146.0-296.4	67.2
water	50.2	43.1	0.0-130.4	16.0
ub/ug/lg	29.5	17.2	0.0-51.6	9.4
marsh	12.5	14.0	0.0-55.6	4.0
ag	5.8	12.4	0.0-50.4	1.9
lb	3.0	7.2	0.0-28.8	0.9
road	2.0	2.2	0.0-5.6	0.6

cavity nests were located in basswood ($n = 3$), red elm ($n = 2$), white elm ($n = 1$), yellow birch (*B. alleghaniensis*) ($n = 1$), and sugar maple (*A. saccharum*) ($n = 1$).

The 0.04 ha and 314 ha circular plot data were taken at 22 and 24 nests, respectively (2 sites were lost to logging before the 0.04 ha plot data were taken). Table 3 lists the means, standard deviations, and ranges of the 15 variables taken at the 0.04 ha plots. The forest types that nest sites were located in are listed in Table 4. Data from the 314 ha circular plots are shown in Table 5. It is important to note that

while the 314 ha plots do not represent the actual habitat utilized by a territorial Barred Owl pair, they can offer something in the way of general habitat assessments. I did not compare used sites against unused sites because I was not able to prove that there were in fact no owls present in areas surrounding the unused sites.

BOX USE BY OTHER WILDLIFE

Detailed notes recording other species use were available on 26 boxes (Table 6), with raccoon and squirrel (3 species) activity predominating. Boxes were used as nest sites by raccoon, squirrel (3 species), wood duck, hooded merganser (*Lophodytes cucullatus*), and vespid wasps (*Hymenoptera*, subfamily *Vespinae*). During fall dispersal, squirrels often placed 25-30 cm of leaf and twig material into the boxes. It was not uncommon to find red or flying squirrels in boxes containing nests made by gray squirrels. Four dead gray squirrels and 1 dead raccoon were found in boxes during January inspections (natural mortalities). Fifty-two percent (52%) of the boxes required annual cleaning; 90% required cleaning at some time or another during the project.

Table 6. Box use by other wildlife.

species	boxes used	visits
Gray Squirrel		
(<i>Sciurus carolinensis</i>)	18	31
Red Squirrel		
(<i>Tamiasciurus hudsonicus</i>)	6	9
Northern Flying Squirrel		
(<i>Glaucomys sabrinus</i>)	6	10
Raccoon	14	18
Porcupine		
(<i>Erethizon dorsatum</i>)	2	4
Wood Duck	4	5
Hooded Merganser	2	2
Northern Flicker		
(<i>Colaptes auratus</i>)	1	1
Vespid Wasp	4	4

DISCUSSION

Data collected during this study reveal that Barred Owls will readily utilize artificial nest boxes, and are willing to tolerate differences in box designs, mounting styles, cavity heights, entrance hole orientation, tree species, tree diameters, tree density, and general habitat features. This should come as no surprise when we understand their need for the limited supply of suitable nest sites - at least in this study area they simply have little choice.

Nest boxes are a viable tool for researching various aspects of Barred Owl ecology. While Barred Owls may function as mature/old growth forest indicator species, the sporadic nesting that was shown in this study suggests that a population monitoring system based on the use of boxes would be inappropriate. Preferred monitoring options may include a taped call/playback response census and/or a system of monitoring the overall mature/old growth forest habitat component.

We have traditionally associated Barred Owls with large tracts of mature lowland hardwoods, such as those found along riverine systems. Nicholls (1973) found 9 radioed Barred Owls to prefer oak and mixed hardwood-conifer habitats in east-central Minnesota. Home ranges averaged 226 ha (range 85-365 ha) in size. In this study, nesting activity occurred predominately in the northern hardwood type, followed by the lowland hardwood, aspen/birch, oak, and jack pine types. Forest types averaged 65 years old and covered 211 ha (67.2%) of the 314 ha plots. The types were basically homogenous, with very few recent canopy disturbances (e.g. logging operations). While our assertion of owls associated with the lowland hardwood type is not incorrect, we perhaps have overlooked the additional habitat provided by the mature northern hardwood, oak, and mixed hardwood-conifer forest types. The owls' use of these types may be a recent condition in Minnesota however, as these maturing types may only now be providing the adequate hunting and nesting areas required by this species. Additional home range/habitat evaluation studies employing radio-telemetry are suggested.

For those interested in putting up Barred Owl boxes I recommend the following:

1. Use 2.5 cm thick untreated/unpainted wood for box material. A 30 x 30 x 50 cm box is adequate. No wire mesh "ladder" is needed inside. Eight or so drain holes should be drilled through the box bottom.
2. Covered boxes should have an entrance hole \geq 18 cm.
3. Topless boxes can be 30 x 30 x 40 cm. Rain and snow did not appear to be a problem for the owls, but access into the 50 cm deep boxes did.
4. Boxes should be placed 7-8 m above ground in a long-lived tree. Trees can be any species and any dbh, but those that provide a 30 m clear flight path to the box (few low limbs or other obstructing vegetation) are desirable.

6. Boxes should be placed in tracts of mature northern hardwoods, lowland hardwoods, or mixed hardwood-conifers (250 ha or larger) in association with water (lakes, ponds, streams, rivers) and openings (upland grass/brush and lowland grass). Some aerial photo interpretation work here will be beneficial in selecting potential box sites. Avoid areas of known Great Horned Owl (*Bubo virginianus*) or Red-tailed Hawk (*Buteo jamaicensis*) activity.
7. To minimize human, corvid, and raccoon encounters with owls, boxes should not be placed within 100 m of a house, field, lake, stream, or road edge, but rather in the forest interior.
8. Nest trees should be spiked for climbing, and wrapped with a 0.7 m wide piece of light metal sheeting (to minimize raccoon predation).
9. Boxes should be cleaned prior to the nesting season, leaving only 5-7 cm of nesting substrate in the box.

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Distribution, Density, and Habitat Relationships of the Barred Owl in Northern New Jersey¹

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Abstract. -- Barred Owls (*Strix varia*) were surveyed in northern New Jersey during a four-year period (1983-86) using vocal imitations (85.5%), tape-recorded calls (8.0%), or non-vocal contacts (6.5%). A total of 62 different locations (territories) were found with a pair responding at 56.5% of locations. Of these locations, 34 were found in an intensive study area (468 sq km) which was systematically searched during the study period. Within this area, one tract of prime habitat (120 sq km) was systematically searched during a single breeding season (1986) and contained 17 locations (0.142 pairs/sq km). The northern half (60 sq km) of this tract contained most of the owl locations (12) and was almost complete wilderness while the southern half contained several suburban housing developments, a major 4-lane highway, and less stands composed of eastern hemlock (*Tsuga canadensis*). Barred Owl habitat was classified visually along 6 different habitat gradients at 36 locations and was compared statistically (Fisher Exact Test) to the habitat at 29 Eastern Screech-Owl (*Otus asio*) and 22 Great Horned Owl (*Bubo virginianus*) locations. Habitat analysis indicated that Barred Owls showed the most preference for mature timber stands, mixed hemlock-hardwood forest, swamps, and proximity to water sources. Barred Owls showed the least preference with regard to areas of extensive forest clearings and proximity to human habitation. Habitat management suggestions are presented based on these findings and the literature. Most critical to Barred Owl success thus far are considered the presence of large remote forest preserves with an abundance of freshwater wetlands and mature timber.

INTRODUCTION

The Barred Owl (*Strix varia*) was listed as a threatened species in New Jersey in 1974 (N.J. Dept. Environmental Protection, Non-game and Endangered Species Project) and has been selected as a management indicator species in some southern Appalachian national forests (Title 36, U.S. Code of Federal Regulations, Sec. 219.19). Given the lack of long-term population surveys of the Barred Owl, however, it is difficult to assess the true status of this owl within its wide range. Simultaneous with this study, Sutton and Sutton (1985) surveyed Barred Owls in southern New Jersey in the coastal plain physiographic province, an ecological subdivision not found in northern New Jersey. They concluded that numbers of Barred Owls were "considerably higher than published accounts intimate" and provided some anecdotal evidence that the population has been increasing in recent decades. In northern New Jersey, the distribution and ecology of the Barred Owl population is not well known, most accounts referring to small localized populations (Stearns 1947, Gutmore 1977, Kane et al. 1985). The pur-

pose of our investigation was to explain the distribution of Barred Owls in northern New Jersey by quantitatively investigating what factors favor or hinder successful inhabitation. In identifying such factors, valuable management insight for maintaining or improving the status of Barred Owls throughout their range might be realized.

STUDY AREA

Northern New Jersey was selected as the study region; it contains three of the four physiographic provinces of New Jersey (Fig. 1). The Piedmont is a relatively flat, low elevation zone of clay and sandstone composition. This region is the most heavily urbanized region in northern New Jersey; some rural areas and parks occur toward its southern end. Forest growth is primarily oak (*Quercus* spp.) and other hardwoods. This region is abutted to the west by the Highlands, a belt of granitic rolling hills with an average elevation of about 300 m. This region is sparsely populated with small villages and towns, but in general, it is heavily forested. While oak predominates much of the region (Beull 1966, Russell 1981), eastern hemlock (*Tsuga canadensis*) and the northern hardwoods Birch-Beech-Maple (*Betula alleghaniensis* - *Fagus grandifolia* - *Acer saccharum*) thrive along ravines, water courses, and plateaus where richer, deeper soils and moisture have accumulated. The Kittatinny Valley extends along the western base of the Highlands and is an area of extensive agriculture, dotted with small rural villages.

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Few tracts of undisturbed forest remain here. The conglomeritic Kittatinny Ridge, however, with an average elevation of about 400 m, is steep and almost entirely forested. Tree composition is mostly oak-pine (*Pinus* spp.) with various associations of northern hardwoods and occasional hemlocks.

Within the study region, an intensive study area (468 sq km) was designated such that it was possible to search virtually the entire area for owl territories during the four-year period, 1983-1986. Within the intensive study area, one area of forest (120 sq km) at the Pequannock Watershed was systematically searched during the 1986 breeding season to determine owl densities since this area represents prime Barred Owl habitat. The northern half of this area is virtually complete wilderness; the southern half was slightly to moderately encroached upon by a few small suburban developments and a major four-lane highway (Route 23), thus providing a good comparison on the effects of land development on Barred Owl density.

METHODS

We began recording Barred Owl locations in the spring of 1983 during a survey of Northern Goshawk (*Accipiter gentilis*) populations in the Highlands (Speiser and Bosakowski 1984). From March-June in 1984, 1985, and 1986 additional Barred Owls were located throughout the study region and the intensive study area. During surveys, either imitated calls (typical eight-note hooting series) or cassette taperecorder broadcasts (Sony CFM-15) were employed for about a 5-min duration or until a response was obtained. If no response occurred within an additional 5-min period, the survey was continued elsewhere. Gould (1977) and Forsman et al. (1984) surveyed populations of Spotted Owls (*Strix occidentalis*) in California and Oregon, respectively, using a combination of vocal imitations and tape-recorded broadcasts. Likewise, Sutton and Sutton (1985) also used both methods to survey Barred Owls in southern New Jersey. Although some other investigators of the Barred Owl have relied completely on the use of cassette tape playback (Gutmore 1978, Smith 1978, Elody 1983,

McGarigal and Fraser 1984, 1985), all have used different equipment, recordings, and sound wattage such that no standardized system has yet been established. Regardless of the method used, most authorities agree that the response of the owl indicates that its breeding territory has been intruded upon (reviewed by Fuller and Mosher 1981) and in the Spotted Owl, at least, only adults that are paired are believed to respond vigorously to calls (Forsman et al. 1977). During the breeding season, this technique has a very good success rate (Table 1) and therefore we consider the possibility of overlooking a breeding territory to be minimal. Since Stearns (1947) and Smith (1978) believed that Barred Owl hooting was audible up to 0.4-0.5 miles, then sampling points can theoretically be spaced as far as one mile (1.6 km) apart to attain systematic coverage of an area as long as calls are given in a radial pattern from the calling source. When owls were found in close proximity (1-2 km) we often were able to verify them as separate pairs/individuals by simultaneous or near simultaneous vocalizations (Forsman et al. 1977, 1984), by obvious natural boundaries (Smith 1978) or by unnatural boundaries such as developments and highways. Furthermore, over half of the owl locations reported here were reconfirmed from one to seven times during the course of the study.

Surveys of other woodland owls were also conducted to serve as a control comparison for analyzing habitat information. Essentially, there are only two other owl species which are common breeders of woodland habitat in northern New Jersey, i.e., the Great Horned Owl (*Bubo virginianus*) and the Eastern Screech-Owl (*Otus asio*). A similar method was used to detect these species, except that Screech-Owl detection was almost completely limited to night surveys (94%) while Great Horned Owls were more often detected during the day

(63%) as were Barred Owls (55%). Although there was some variability in location methods, the sample size for each species was large (22 - 36 different territories), and vast areas of habitat were sampled during the four-year study period. Due to the multi-dimensional habitat parameters involved, it was impossible to quantify search effort spent in all the various habitat types encountered; however, we deliberately tried to avoid search bias for each species such that relative comparisons among all species were meaningful.

Table 1. -- Response rate of Barred Owls to imitated or taped calls at some known traditional breeding locations with span of years of first and last known response given in parentheses. Note that these data represent the minimal response rates since a non-response may have been due to the death or permanent relocation of the owl(s).

Location	Breeding Season		Non-Breeding Season	
	no. of re-checks	no. of responses	no. of re-checks	no. of responses
<i>Wanaque FWMA</i>				
Jennings Creek (1980-1985)	2	2	1	0
unnamed creek (1983-1985)	1	1	-	-
Beech Creek (1980-1984)	4	4	2	2
Hewitt Brook (1984-1986)	4	3	2	0
Norvin Green SF (1984)	1	1	3	0
<i>Pequannock Watershed</i>				
Cedar Pond (1983-1986)	5	5	2	0
Dunkers Pond (1986)	1	0	-	-
Henderson Road (1986)	2	2	-	-
Henderson Road North (1986)	2	1	-	-
Lake Stockholm (1986)	1	1	-	-
Timber Creek (1986)	2	1	-	-
Tenaco Pipeline (1985-1986)	1	1	-	-
Hanks Pond (1986)	-	-	1	1
<i>Sterling Forest (New York)</i>				
Sterling Lake (1978-1985)	2	1	4	1
Cedar Pond (1978-1985)	-	-	3	2
<i>High Point State Park</i>				
Sawmill Lake (1983-1986)	1	1	-	-
Parker Brook (1986)	1	1	-	-
<i>Great Swamp NWR (1979-1985)</i>				
New Vernon Road	1	1	-	-
Woodland Road	1	1	-	-
Meyersville Road	1	1	-	-
White Bridge Road	1	0	-	-
Totals	34	28	18	6
Response Rate	82.4%		33.3% *	

abbreviations: FWMA = fish and wildlife management area, SF = state forest, NWR = national wildlife refuge. * = significantly different than response during breeding season (Fisher Exact Test, $p = 0.0007$).

Table 2. -- Habitat classification system for northern New Jersey owl sightings. For each owl location, one selection was made from each category which best described the habitat within a 100 m radius of the point where the owl(s) was first detected. If more than one choice was applicable, then the two most prevalent types were selected, each given a value of (0.5).

SUCCESSIONAL STAGE:

1. young field - low herbaceous plant cover only.
2. old field - mixed herbaceous cover with up to 50% shrub cover.
3. shrubland - low thickly-growing woody-stemmed plants (shrubs) covering over 50% of area.
4. young forest - saplings and poles mostly less than 15 cm in DBH.
5. submature forest - moderate-aged stands mostly between 15-30 cm in DBH.
6. mature forest - oldest stands mostly over 30 cm in DBH (including old-growth).

DOMINANT TIMBER TYPE:

1. Oak-Hardwood - (*Quercus* spp., *Carya* spp., *Fraxinus americana*, *Acer rubrum*, *Betula lenta*, *Tilia americana*, *Liriodendron tulipifera*, *Prunus serotina*, *Nyssa sylvatica*).
2. Northern Hardwood - (*Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*)
3. Hemlock - (*Tsuga canadensis*)
4. Pine - (*Pinus strobus*, *P. resinosa*, *P. sylvestris*, *P. rigida*)
5. Spruce - (*Picea abies*)
6. Cedar - (*Chamaecyparis thyoides*, *Thuja occidentalis*, *Juniperus virginiana*)

TOPOGRAPHICAL TYPE:

1. lakeshore - terrestrial community found on the edge of open bodies of water.
2. marsh - inundated land with emergent herbaceous plants.
3. swamp - permanently flooded timber stands, frequently containing dead wood.
4. riverine - floodplain forest, alluvial basins, valleys, gorges.
5. upland - well-drained plateaus, ridges, upper slopes.

CLEARINGS (percent estimate, select only one)

1. none
2. trail/road represents only clearing
3. <10%
4. 10-50%
5. 50-100%

DISTANCE TO WATER SOURCE and HUMAN HABITATION

(select one choice for each of these two categories)

1. 0-100 m
2. 100-500 m
3. >500 m

DBH = diameter at breast height.

All owl locations were plotted on detailed local or regional maps and the habitat was classified according to the categories defined in Table 2. In most cases, habitat classification was achieved with visual estimates in the field; actual measurement was needed only for a few borderline cases. All habitat classifications were made by the first author to avoid interobserver variability (Lehner 1979). Only one habitat profile was made per owl territory; 26 Barred Owl territories were not quantified. The Fisher Exact Test was used to test for differences in proportions (Zar 1974) between the Barred Owl sample population and the two control species (Great Horned Owl and Screech-Owl). Barred Owl locations were

transferred to a section of a road map (Travel Vision Map, General Drafting Co., Convent Station, N.J.) to provide a general distribution map. Pellets found at a Barred Owl winter roost site were examined quantitatively by counting the number of skulls and mandibles (divided by 2) as described in Marti (1974).

RESULTS

Censusing

A total of 62 Barred Owl locations (territories) was recorded during the study period 1983-1986 (Fig. 1): 53 with imitated calls, 5 with cassette tape broadcasts, 2 calling on own, and 2 visual sightings. Barred Owl locations were intentionally found during the breeding season (58) with only five locations found during non-breeding months. At 35 locations (56.5%), the owl was joined by its mate (total = 97 owls), although at a few single locations a pair was known to be present before the study period. Apparently, both owls will not always respond vocally, especially since the female might be incubating or brooding young and may be reluctant to call (Devereux and Mosher 1982). Furthermore, we noted that it frequently required a longer period of continued owl broadcasts (5 to 15 min) to prompt the second owl (presumably the female) into calling. Since our broadcasts were generally of shorter duration, this may also help explain why more than one-third of the owls did not show evidence of being paired adults. Similarly, Smith (1978) found pair response at 64% of Barred Owl locations in New England. In the Spotted Owl, Gould (1977) found pair response at only 34.5% of locations. Barred Owl response to calls was greatest during the breeding season (Table 1) and showed no obvious dependence on time (am or pm) or cloud cover. In addition, we also found that pair responses were more frequent during the breeding season (Table 3) and none occurred during winter.

Table 3. -- Seasonal variation in the frequency of paired and single Barred Owl responses (data includes repeated trials at some locations).

	single	pair
Jan	3	0
Feb	1	1
Mar	10	12
Apr	16	16
May	21	9
Jun	11	11
Jul	4	2
Aug	0	1
Sep	2	0
Oct	2	1
Nov	1	0
Dec	4	0

Territorial Behavior

In most cases, Barred Owls responded vocally well before they arrived to our calling site, but occasionally they flew-in silently to investigate us. Even though we usually wore inconspicuous clothing and tried to hide in available brush, most owls were shy and would generally remain well hidden while calling. If they caught a glimpse of us, they would usually flush and become silent or call from a safer distance. Only on six occasions did they

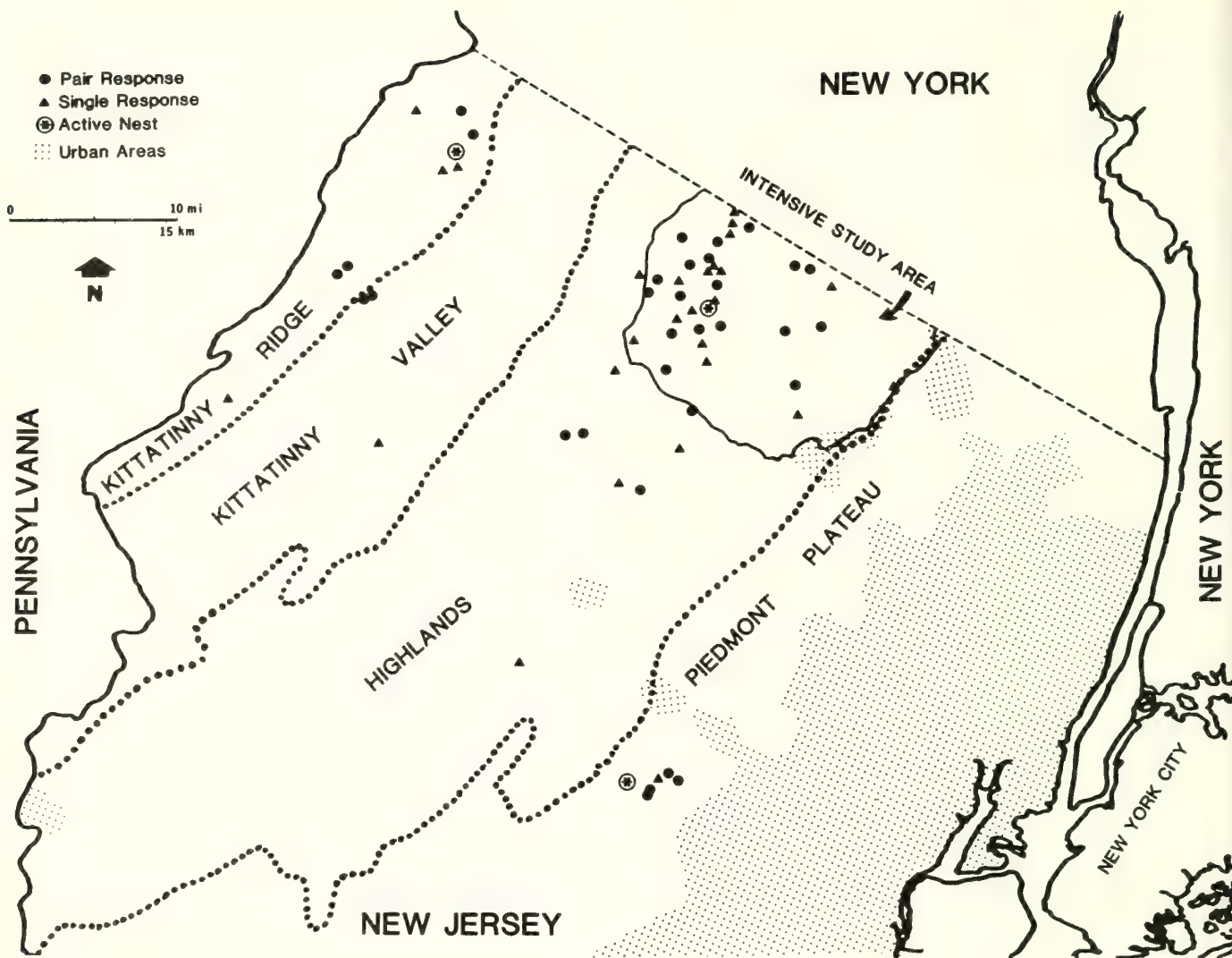


Figure 1. -- Map of northern New Jersey showing major physiographic subdivisions and distribution of Barred Owls from 1983-1986. Intensive study area was systematically searched during this period.

continue calling and almost completely ignore our presence even when we were in direct view. When a pair was present, they frequently perched close-by (often in the same tree) and began an extremely loud chorus of howls, hoots, shrieks, and tremulous wailings, often in rapid succession. On one occasion, two of us were well hidden while calling and decided to challenge a pair of chorusing owls with our own vocal imitation. This caused the owls to stop vocalizing momentarily, but in less than one minute, they began again. The owls sounded as if they were agitated by our response and continued to respond alternately to our challenge, frequently cutting us off before we had finished a complete chorus (15-20 sec). This vocal battle lasted nearly 15 minutes until one of the owls moved closer and saw us. These observations suggested to us that the owls were completely fooled by our imitated calls, and as such, protested strongly against intrusion by what they presumed to be conspecifics.

Density

In the intensive study area, 34 locations were found during the period (0.073 pairs/sq km), many of which were known to be traditional sites (see Table 1). We believe this figure to be very close to the total breeding population of the area since virtually all suitable woodlands were carefully censused during the four-year period. Unsuitable areas that were not checked were places such as high density suburban zones, industrial and commercial areas, and other high human-use areas such as ball fields, camps, bathing beaches, marinas. Barred Owls are considered non-migratory permanent residents by most authorities (Bent 1938, Bull 1964) and presumably retain the same area as a territory for many years (see dates in Table 1). In support of our observations, Bent (1938) reported that several Barred Owl territories remained occupied for over 30 years. Similarly, Forsman et al. (1984) believed that the Spotted Owl occupies its territory for life and noted 5 cases where marked individuals that disappeared were replaced the following spring. Therefore, we do not believe that the four-year study period produced an inaccurate estimate of the total owl population in

the intensive study area due to frequent relocation of existing pairs. Most of the Barred Owl territories were distributed in the western half of the intensive study area (Fig. 1) which was much less developed.

In the Pequannock Watershed study area, a total of 17 locations was found during the 1986 breeding season (Fig. 2): at 8 locations a pair responded (47%), at 7 sites a single resident responded on at least two different occasions (female may have been incubating or brooding young), and at 2 sites only a single response was obtained (sites not rechecked - may well be residents). Assuming that all locations represented paired adults (see rationale in methods section), then the density of the 120 sq km area was 0.142 pairs/sq km and the mean nearest-neighbor distance was 1.96 km (CV = 49.5%).

Distribution

Barred Owls occurred in all four major physiographic regions of northern New Jersey (Fig. 1). Although southern areas were less intensively searched, regional reports (Hanisek 1984, Kane and Valent 1986) verify that few Barred Owls inhabit the southern Piedmont, southern Highlands, and Kittatinny Valley. In the Piedmont, the small but dense population are traditional residents of the Great Swamp National Wildlife Refuge (2800 ha) vicinity and few are known to exist elsewhere in this region due to heavy urbanization and development impacts. The Highlands population, the largest, is not just the result of more intense search effort, but also reflects the presence of many large forest preserves in the northern end: Pequannock Watershed (14000 ha) with adjacent Wawayanda State Park (4200 ha), Wanaque Fish and Wildlife Management Area, Sterling Forest (private), Mahlin Dickerson County Reservation (520 ha), Norvin Green State Forest, and Piccatinny Arsenal (U.S. Army). At the southern end, the Highlands is mostly privately owned with increasing amounts of farmland, second-growth stands, and much greater fragmentation of woodlands. In the adjacent Kittatinny Valley, this trend is true throughout its entire extent with even more intense agriculture and virtually no forest preserves, hence, explaining the low number of Barred Owl locations. The Kittatinny Ridge, the smallest region, is mostly state and federal land and nearly all the land is forested. Accordingly, Barred Owl abundance was relatively good (9 locations) considering the small size of this region. The fewer number of owls near the southern end of this region was considered the result of the increasing steepness of the ridge which resulted in fewer wetlands and stunted xeric oak forests.

Habitat Analysis

Most Barred Owls were located in mature timber stands, as opposed to Screech-Owls, found more often in other successional stages, and Great Horned Owls, found more in young field habitat (Fig. 3a). Barred Owls were encountered less often in oak-hardwood stands than Screech-Owls and Great Horned Owls, and were more often in hemlocks (Fig. 3b). Barred Owls were more often found in northern hardwoods than Screech-Owls but not significantly different from Great Horned Owls. The relative amount of clearings within the stands showed that Barred Owls were found more frequently in areas with no clearings or trail only when compared to the other woodland owls (Fig. 3c). Conversely, Barred Owls were observed significantly less in areas with greater than 10% clearings. The most significant topographical difference was that of Barred Owl abundance in swamps (Fig. 3d) when compared to Screech-Owls or Great Horned Owls. In upland habitat, Barred Owls were found significantly less often than Great Horned Owls. Barred Owls were found significantly closer to water sources than Great Horned Owls (Fig. 3e) and only slightly closer than Screech-Owls (not significant). Barred Owls were less often within 100 m of human habitation (Fig. 3f) when compared to Screech-Owls and Great Horned Owls and favored sites that were greater than 500 m when compared to these owls. Screech-Owls showed the reverse trend - actually favoring woodlands with nearby human habitation. Great Horned Owls showed neither an avoidance nor preference with regard to their proximity to human habitation.

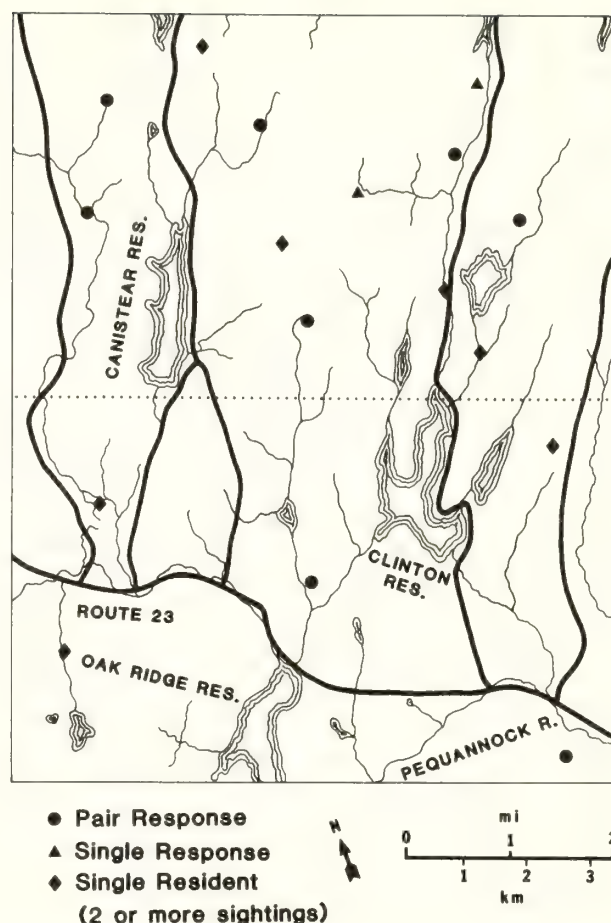


Figure 2. -- Distribution of Barred Owls in the 120 sq km Pequannock Watershed study area during 1986 breeding season. Although the area was systematically searched, note that the density of owls (12 territories) was much greater in the northern half of the area which was almost complete wilderness (above dotted line). In contrast, the southern half contained a major highway (Route 23), several suburban housing developments, and less stands containing eastern hemlocks, and only 5 territories were established. Average nearest-neighbor distance for the northern half was 1.48 km (CV = 17.6%) and 3.09 km (CV = 35.3%) for the southern half.

Table 4. -- Analysis of 34 Barred Owl pellets from winter roost at the Great Swamp National Wildlife Refuge, Meyersville, 1985-86.

Mammals	number
Short-tailed Shrew (<i>Blarina brevicauda</i>)	5
Siamose Mole (<i>Condylura cristata</i>)	1
Meadow Vole (<i>Microtus pennsylvanicus</i>)	18
White-footed Mouse (<i>Peromyscus leucopus</i>)	2
Southern Flying Squirrel (<i>Glaucomys volans</i>)	1
Birds	
Blue Jay (<i>Cyanocitta cristata</i>)	2
Invertebrates	
Crayfish (<i>Cambarus sp.</i>)	2
Total Prey Items	31
Prey Items/Pellet	0.91

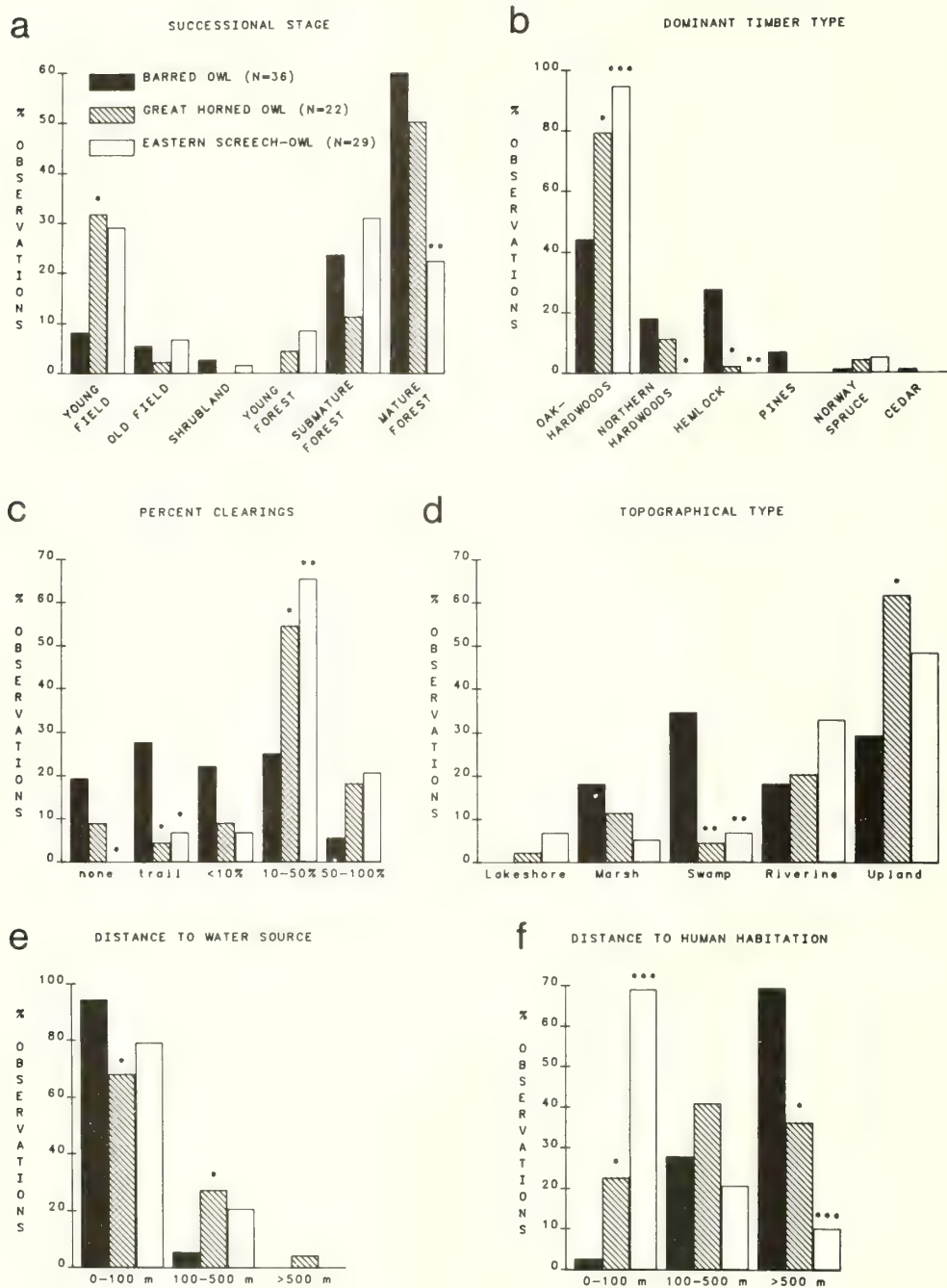


Figure 3. -- Habitat comparison of Barred Owl to two other sympatric woodland owl species in northern New Jersey. See Table 2 for description of habitat variables. Asterisks indicate a statistically significant difference from Barred Owl population (Fisher Exact Test, *** $p < .001$, ** $p < .01$, * $p < .05$).

Only three Barred Owl nests were found during the study. All were in large holes of large dead trees and included white oak (*Quercus alba*), sugar maple (*Acer saccharum*) and black willow (*Salix nigra*). Despite careful checking of all large stick nests found during this and other raptor studies (Speiser and Bosakowski 1984, 1987) we have never observed these nests to be used by Barred Owls as has been reported elsewhere (Bent 1938). Apparently, cavity availability is adequate in the woodlands presently occupied by Barred Owls in northern New Jersey.

Food Habits

Thirty-one food items were identified from pellets collected at a Barred Owl winter roost (Table 4). The roost was situated in a Norway spruce (*Picea abies*) grove that bordered extensive old fields and open marsh, hence explaining the abundance of meadow voles taken. Unfortunately, not enough pellets were found at nest sites or other habitats to make a valid comparison among different habitat types. However, our data are in close agreement with some other food habits studies (Wilson 1938, Rusling 1951, Marks et al. 1984) which indicate that the Barred Owl might occasionally be a "specialist" on *Microtus*.

DISCUSSION

A total of 97 Barred Owls was detected on 62 territories during the study period 1983-1986. Only 5 of these locations were found during non-breeding months, but because the Barred Owl is a permanent resident, it is likely that these owls were defending permanent home ranges as indicated by other known breeding localities that were "defended" during winter (Elody 1983, this study - Table 1). When a pair responded (56.5% of locations), they usually began calling alternately with the typical eight-note hooting series which was almost always followed by a loud and frenzied chorus. Although other authors have noted this duetting (Bent 1938, Fitzpatrick 1975, Smith 1978, Devereux and Mosher 1982, Elody 1983, McGarigal and Fraser 1985), usually referred to it as "caterwauling", its purpose is poorly understood, save for the fact that it reveals the location and emotional level of the owls (Elody 1983). Of interest, we noted that this chorus was only elicited when the owls were in very close proximity to each other. Likewise, Devereux and Mosher (1982) once observed caterwauling just prior to a food exchange near a nest. Perhaps this behavior functions in mate recognition, strengthening the pair-bond and warning intruders that a pair-bond has already been established. Because these choruses were very loud and frequently given in response to our calling, this behavior seems to also have a strong territorial function, possibly supplemental to the typical 8-note call. Outside of the breeding season, the response rate of Barred Owls to calls decreases dramatically (Smith 1978, Elody 1983, this study), thus making winter census results, such as the Christmas Bird Counts, unreliable. We also found only single responses during the winter months with pairs responding primarily during the breeding season (March to June).

The intensive study area yielded 34 Barred Owl locations (0.073 pairs/sq km) during 1983-1986. The Pequannock Watershed study area, located in one of the more remote sections of the intensive study area, was occupied at 17 locations in 1986 (0.142 pairs/sq km). The latter density is comparable to Smith's (1978) data from two selected study areas (7320 ha) in New England from which we calculated densities of 0.147 (New Hampshire) and 0.191 (Connecticut). In northern Michigan, a wilderness area (9308 ha) with prime habitat (climax hemlock-northern hardwoods) was censused and found to contain a density of 0.355 (Elody 1983). If we consider the density of owls in the northern half of Figure 2 (60 sq km), where there is no highway, almost total wilderness, and more stands containing hemlock, then our owl density figures increase from 0.142 to .206, 56% of the saturation level in Elody's (1983) study area.

Most Barred Owls were observed in mature timber stands, whereas the majority of Screech-Owls inhabited younger successional stages. Great Horned Owls were found only slightly less in mature forests than Barred Owl, but were much more often associated with young fields. In Virginia, McGarigal and Fraser (1984) found that 25 Barred Owls more frequently preferred old stands (>80 yrs old) rather than young stands (<80 yrs old). In the central Appalachians, Devereux and Mosher (1984) found that Barred Owl nests (N=8) were in more mature forests than 76 random sites. Similarly, Forsman et al. (1977, 1984) found higher densities of Spotted Owls (the western congener of the Barred Owl) in old-growth forests versus young forests. In southern New Jersey, Sutton and Sutton (1985) also noted a strong association of Barred Owls with "the oldest growth and uncut stands ... of hardwood forest" although no quantitative tree data was obtained. The requirement of Barred Owls for mature woods reflects their need for large dead trees with nesting cavities (Devereux and Mosher 1984). It is also hypothesized that these forests provide clear unobstructed flight paths (little or no understory) for hunting and better prey vulnerability (Nicholls and Warner 1972, Elody 1983, Devereux and Mosher 1984).

Barred Owls have been noted to prefer mixed woods in northern latitudes (Wilson 1938, Smith 1978, Tyler and Phillips 1978, Elody 1983). This preference concurs with our findings in that Barred Owls were found in hemlock stands more frequently than the other two woodland owls. Elody (1983) concluded that coniferous growth was important to Barred Owls because it provides dense forest cover to prevent mobbing by birds and may also provide an escape medium (Carter 1925, Stirling 1970). However, this rationale does not explain why coniferous growth was not used as much by the other two owl species in our study. D.G. Smith and Gilbert (1984) noted that Screech-Owl use of evergreen cover occurred mainly during winter months which supports our observations. The distribution of mixed forest is limited mainly to the northern Highlands and sections of the Kittatinny Ridge, however, conifers are apparently not an essential requirement since more than half of the Barred Owls were found in deciduous stands (e.g., the Great Swamp maintains a dense population of Barred Owls and only a few cedars and planted conifers are available.)

In this study, Barred Owls tended to avoid areas with extensive clearings as compared to Screech and Great Horned Owls. Nicholls and Warner (1972) showed evidence that fields and open marsh habitat were avoided. Fuller's (1979) data from the same study area (radiotelemetry location every min, instead of every 15 min) showed a greater individual use of fields (5-33.3%). Devereux and Mosher (1984) found eight nests to be significantly closer to edge than random sites. Most of the Barred Owls we encountered were in deep forests with fewer and smaller clearings than Great Horned Owl or Screech-Owl territories. Our findings corroborate those of Elody (1983) who has reported the highest known breeding density of Barred Owls. He noted that forest cover was mostly contiguous with very few openings.

The major topographical difference that we found for the Barred Owl in comparison to the other owls was the preference for swamps (and other associated wetlands). Most of the literature supports this association with wet areas (Carter 1925, Errington and McDonald 1937, Bent 1938, Stearns 1947, Applegate 1975, Soucy 1976, Elody 1983, Sutton and Sutton 1985). Fuller (1979) found dense lowland habitats were used more frequently during reduced activity periods, and both marshes and swamps were used if available. Elody (1983) found a positive correlation with marsh use of seven radio-tagged owls. In southern New Jersey, Sutton and Sutton (1985) independently came to the same conclusion as we did that Barred Owls preferred freshwater wetland forest habitat over dry woodlands. Besides being avoided by human intrusion, we contend that swamps and marshes were almost always associated with a greater abundance and diversity of prey species (birds, small mammals, amphibians, crayfish, fish) than other topographical types in our region.

As expected on the basis of preference for wetlands, the Barred Owl was found closest to water sources, significantly closer than Great Horned Owl, but not Screech-Owl. The latter result is not unexpected since Ellison (1980) found a significant positive correlation between running water and Screech-Owl habitat use in Massachusetts. Apparently, water is also an important habitat component for Barred Owls as well. Karalus and Eckert (1974), Bolles (1890), and others have noted that water sources are frequently used for drinking and bathing, and the inclusion of crayfish, fish, and amphibians in the diet (Errington 1932, Rusling 1951, Korschgen and Stuart 1972, D.G. Smith et al. 1983, Devereux and Mosher 1984, this study - Table 4) indicate the use of water as a hunting habitat as well. Of interest, Gould (1974) reported that 90% of Spotted Owls were found within 0.2 miles of water and Forsman et al. (1984) found 85% of Spotted Owl nests within 250 m of water.

The Barred Owl was found to be the most sensitive of the three owl species regarding proximity to human habitation (and hence, disturbance). This result agrees with Smith (1978) who found a negative correlation of Barred Owl occurrence with human dwellings in Connecticut and New Hampshire. In southern New Jersey, Sutton and Sutton (1985) also noted qualitatively that Barred Owls were "located as far from human habitation as possible". On the other hand, our finding of Screech-Owl preference for proximity to human habitation concurs with the finding of D.G. Smith and Gilbert (1984) that Screech-Owls significantly over-utilized suburban lawns as a habitat type. Below we have submitted several explanations which should help explain this phenomenon: (1) Screech-Owls can avoid predation from Barred Owls (Errington 1932, Bent 1938, Rusling 1951) by inhabiting woodlands on the edge of suburban neighborhoods, (2) the lack of Barred Owl (and other raptors) in these areas decreases potential competition for food sources (note large overlap in prey use of Screech-Owl in Rusling 1951 and Barred Owl in this study - Table 4), (3) trimmed lawns provide excellent prey vulnerability for the owls (easy capture, lack of cover, loss of concealment by prey), (4) Human activities and structures tend to proliferate certain prey species (lawns - moles, lights - moths, garbage - rodents). In contrast, the Barred Owls' success in northern New Jersey results largely from the existence of large remote forest preserves, especially those lands that have minimal signs of human impact. Hence, we consider true wilderness areas as an essential requirement for the maintenance of healthy Barred Owl populations.

MANAGEMENT IMPLICATIONS

The optimal habitat profile for the Barred Owl is: large contiguous forests of mature and old-growth timber, mixed with hemlock, interspersed with a variety of wetland types and free of human dwellings, roads, or other unnatural disruption. We recommend that such areas be acquired as public properties and set aside as wilderness with no human manipulation of habitat. Existing public lands possessing these characteristics should not be subjected to any kind of thinning, selective or clearcutting. One of the primary arguments against logging these areas is that the creation of cleared areas will favor the invasion of the larger, more aggressive Great Horned Owl, which has been known to prey upon the Barred Owl (Bent 1938) and certainly compete for food and nesting sites. Similarly, McGarigal and Fraser (1984) noted that the Great Horned Owl will benefit if old stands are adjacent to farmland. Selective cutting of optimum habitat is also not advisable since these areas are needed as population reserves for continued replenishment of marginal habitats.

At young and submature stands, we suggest careful thinning procedures should be used for accelerating the growth of larger trees and providing the flyway space below the canopy needed by Barred Owls. Such sites, if large enough in area (at least 400 ha/pair), could become potential breeding habitat within a few decades,

especially if situated near wetlands. Dry mountain ridgetops and upper slopes are not of any apparent value to Barred Owls and these should be considered if timber harvesting or development is desired. Unfortunately, this type of terrain is seldom desirable for construction as humans usually prefer valleys and flatlands similar to areas that would be suitable for the Barred Owl. Hence, future land development remains the biggest threat to this species since our findings clearly indicate that human habitation drastically reduces habitat suitability.

Similar to our findings, Smith (1978) noted that Barred Owls always avoided suburban developments even when the canopy was virtually uninterrupted. She suggested that multifamily dwellings be considered in place of even-spaced suburban neighborhoods which waste much more valuable space. For future development, careful assessment of alternative construction sites should be encouraged to prevent further encroachment on (or fragmentation of) our valuable wilderness areas.

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Ecology of the Three Species of *Strix* Owls in Finland¹

Heimo Mikkola²

The Tawny, Ural, and Great Grey Owls breed sympatrically in large areas in the USSR, south-eastern Poland, and Finland. In Finland their area of sympatry covers, especially in good vole years, almost the entire southern and central country. This presentation concentrates on four ecological parameters: activity, food, breeding habitat, and nest site.

The southern Tawny Owl is the most nocturnal in the breeding season. The northern limit of its range may be determined by the short summer nights. In contrast, the northern Great Grey Owl is the most diurnal species, which has adapted to light summer nights in its central range by being active throughout the day and night, only ceasing to feed its young in the afternoon. The Ural Owl has an intermediate position, showing a biphasic activity, with the highest peak in the late evening and lower peak in the early morning, and, to a small extent, remaining active also during the day.

The Great Grey Owl, which is the largest, is a small rodent specialist. Both Ural and Tawny

Owls are catholic predators and food generalists. Their food niches are about 2.5 times broader than that of the Great Grey.

Great Grey Owl breeding habitat is the most catholic among the three; it breeds in forests of all kinds. Habitat selection of the Tawny is the most restricted, but overlaps extensively with that of the Ural Owl. The Tawny Owl is almost exclusively a hole-nester (92% of nest sites studied), while nest selection by the Ural Owl is quite catholic, including nest boxes and holes (53%), stumps (23%), and twig nests (20%). The Great Grey Owl uses mainly twig nests (79%) and stumps (13%), and may even lay eggs on the ground (3%). Therefore, Great Grey and Tawny Owls are not competing for the same nest sites, while competition for nest sites may be keen between Ural and Tawny Owls. Occasional competition between Great Grey and Ural Owls may also occur.

As measured by the four aforementioned parameters, the Ural Owl has the widest niche, that of Tawny being 73% and that of the Great Grey only 48% of the niche of the first-mentioned. These results suggest that competition among the three species is common, and should be taken into account when providing artificial nest sites. Favouring one of the species may harm another. Similar competition is likely to exist between Barred and Spotted Owls, but more research is needed to quantify these niche relationships.

1 Summary of paper presented at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 2-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

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Home Range Size of Hawk Owls: Dependence on Calculation Method, Number of Tracking Days, and Number of Plotted Perchings¹

Bjørn T. Bækken, Jan O. Nybo, and Geir A. Sonerud²

Abstract.---Three nesting males and two non-nesting females of the Hawk Owl were equipped with radio transmitters and tracked for 3-11 weeks during 1984-85 in the northern boreal zone of southeast Norway. Home range sizes were larger when calculated by the convex polygon method than when calculated by the quadrature method (squares of 250 m x 250 m). Home range size as calculated by the convex polygon method increased with number of tracking days, while that calculated by the quadrature method increased with number of perchings plotted.

INTRODUCTION

The introduction of radio telemetry has made it possible to sample data on home range use of animals that move over large areas. Some of the first studies making use of this technique dealt with owls (Nicholls and Warner 1972, Forbes and Warner 1974). Since then several studies on the ecology of owls involving radio telemetry have been conducted, mainly in North America. In Europe few such studies have been made (Nilsson 1977, 1978, Wijnandts 1984, Sonerud et al. 1986, Jacobsen and Sonerud 1987).

Shape and size of recorded home ranges for owls may vary depending on several factors connected with data sampling and calculation method. For instance, it may differ depending on whether the owls are located during their usually nocturnal hunting or during their diurnal roosting (Wijnandts 1984, Jacobsen and Sonerud 1987), and may also depend on sample size and sampling interval (Swihart and Slade 1985), and the calculation method (Föhrenbach 1984).

Hawk Owls *Surnia ulula* search for food also during the day (e.g. Glutz von Blotzheim and Bauer 1980). Hence, a realistic estimate of their home range size should be obtainable by diurnal radio-tracking only, in contrast to e.g. Tengmalm's Owls *Aegolius funereus*, for which diurnal and nocturnal activity level, and therefore also home ranges, differ markedly (Jacobsen and Sonerud 1987). Here we report the home range sizes of 5 Hawk Owls as calculated by two dif-

ferent methods, and relate these estimates to the sample sizes, viz. number of days tracking the owl and number of owl perchings plotted.

STUDY AREA

The study was conducted during 1984-85 within an area of 70 km² at an altitude of 520-720 m in the northern boreal zone (sensu Anonymous 1977) in Hedmark county, southeast Norway (61°00'N, 11°10'E). The study area consists of coniferous forest with Norway Spruce *Picea abies* dominating, mixed with bogs and fens. The area is usually covered by snow from mid-November to mid-May. In 1984 the snow-melt occurred extremely early, and in 1985 extremely late, with clear-cuts being snow-free May 1 and 25, respectively.

METHODS

Three male Hawk Owls trapped in mist nets at the nest site (M1 in 1984, M2 and M3 in 1985), and two female Hawk Owls trapped in a bow-net outside the nesting season (F1 in 1984 and F2 in 1985), were equipped with radio transmitters (Biotrack, England) mounted as a back-pack (fig. 1), and tracked 3-11 weeks (table 1). The tracking was conducted during daytime by first localizing, and then following, the hunting owls by walking or skiing, using a hand-held receiver (Televilt, Sweden) and a 4-element yagi-antenna. All observed perchings of the owls were plotted on aerial photos with scale 1:15,000 in the field, and later plotted on maps with scale 1:5,000. Since an important aim of the tracking was to sample data on the foraging behavior of the owls, each owl was followed as continuously as possible for several hours per day. The average number of perchings plotted per day varied from 2-54 for the five owls, with an average of 19. Hence, the plottings of perched owls were to a large extent autocorrelated, and

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only non-statistical methods could be employed for estimating home range size as long as all plotted perchings were included (see Swihart and Slade 1985). Therefore, home range sizes were calculated in two ways: 1) By the convex polygon method (Mohr 1947, Föhrenbach 1984), and 2) by the quadrature method (Föhrenbach 1984), dividing the home range into squares (250 m x 250 m) and counting all squares with plottings of perched owls.

We tried to generate more independent, i.e. less autocorrelated, plottings by limiting the sample size to only the first plotting each tracking day. However, this decreased the sample size of some of the owls to such an extent that the calculated home range size amounted to only a small fraction of the size calculated when all plottings were used. Therefore, we included all plotted perchings of the Hawk Owls in our calculations of home range size. Swihart and Slade (1985) also found that over a specified time frame nonstatistic estimates became increasingly accurate with increasing sample size, even when autocorrelation increased.



Figure 1.--Hawk Owl M3 is released after being equipped with a radio transmitter. Photography by G.A. Sonerud.

Table. 1.--Home range size, as estimated by the convex polygon method and the quadrature method, for 5 Hawk Owls (M=male, F=female), with tracking period, number of tracking days, and number of plotted perchings shown.

Owl	Tracking period	Home-range size (ha)		Tracking effort	
		Polygon	Quadrature	Days	Plotted perchings
M1	May 28-June 22/84	390	344	12	653
F1	Sept. 15-Nov. 6/84	264	275	12	276
F2	Jan. 10-March 28/85	848	156	22	42
M2	April 29-June 6/85	217	131	7	57
M3	May 15-June 5/85	140	106	5	59

RESULTS

Home range size of the five Hawk Owls varied from 140-848 ha, with an average of 372 ha (S.D. = 281), when calculated by the convex polygon method, and from 106-344 ha, with an average of 202 ha (S.D. = 102), when calculated by the quadrature method (table 1). The home range sizes calculated by the convex polygon method were almost significantly larger than those calculated by the quadrature method (table 1; $T_5=1$, $n=5$, $p=0.06$, Wilcoxon's matched pairs signed-ranks test (Sokal and Rohlf 1969)), and there was no significant correlation between the home range sizes as calculated by the two methods (table 1; $r_s=0.07$, $n=5$, $p>0.1$, Spearman's rank correlation test, one-tailed (Siegel 1956)). However, if we exclude the owl tracked when the ground was snow-covered (F2) there was a significantly positive correlation between home-range sizes as calculated by the two methods (table 1; $r_s=1.00$, $n=4$, $p<0.05$). The shape and relative size of the home range of each owl as calculated by the two methods are shown in figure 2.

Cumulative home range size as calculated by the convex polygon method levelled off during the tracking period for all individuals except F2 (fig. 3). This suggests that the total home range size found was close to the real one for the three nesting males tracked as well as for the female tracked during autumn, but possibly not for the female tracked during winter. Total home range size as calculated by the polygon method was significantly linearly correlated with number of tracking days ($r=0.97$, $n=5$, $p<0.01$ (Sokal and Rohlf 1969)), while the total home range size as calculated by the quadrature method was not ($r=0.21$, $n=5$, $p>0.1$). There was no significant linear correlation between home range size as calculated by the polygon method and the number of plotted perchings ($r=-0.07$, $n=5$, $p>0.1$). However, the linear correlation between total home range size, as calculated by the quadrature method, and number of plotted perchings was significant ($r=0.94$, $n=5$, $p<0.01$).

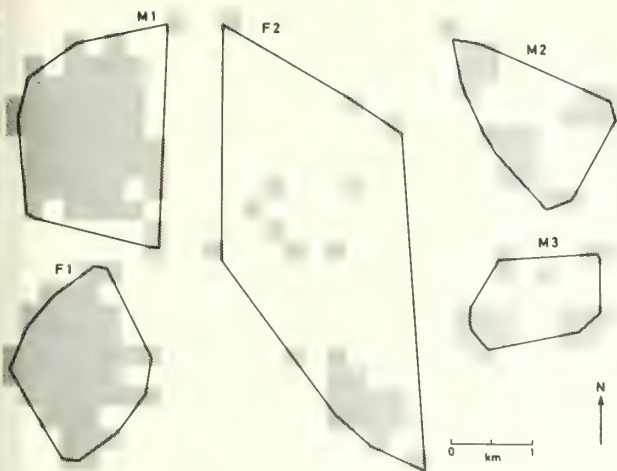


Figure 2.--Relative size and shape of the recorded home ranges of 5 Hawk-Owls (M=male, F=female) as calculated by the convex polygon method (solid line) and the quadrate method (shaded squares).

DISCUSSION

Home range size varied substantially among the 5 Hawk Owls, especially when calculated by the convex polygon method. Great individual variation in home range size was also found in Barred Owl *Strix varia* (Nicholls and Warner 1972), Wolverine *Gulo gulo* (Whitman et al. 1985) and Bobcat *Felis rufus* (Fuller et al. 1985). This may be explained by different home range use by the sexes (Whitman et al. 1986), or by sampling data in different seasons (Fuller et al. 1985). Nicholls and Warner (1972) found that Barred Owls had a strong preference for certain habitat types and avoidance of others, so that the home range size may have depended on the spacing of preferred habitat patches. In our study, most of the variation in home range size may be explained by differences in the sample sizes between individuals.

There was a positive linear correlation between the convex polygon home range size and the number of tracking days. The cumulative home range size clearly levelled off for the two individuals tracked for 12 days each, indicating that this effort may give a good estimate of an Hawk Owl's home range size. The large home range size, as calculated by the convex polygon method, for one female was mostly due to a home range shift in the last part of the tracking period. This was the only Hawk Owl that was followed during the winter. Similarly, the cumulative home range sizes of 3 Eastern Screech Owls *Otus asio* in Connecticut, USA, and one Tengmalm's Owl in Norway, continued to increase throughout the time monitored (Smith and Gilbert 1984, Jacobsen and Sonerud 1987). Further, microtine rodent prey are less available on snow-covered than on snow-free ground (Sonerud 1986), and this should induce a larger home range in winter than in other seasons.

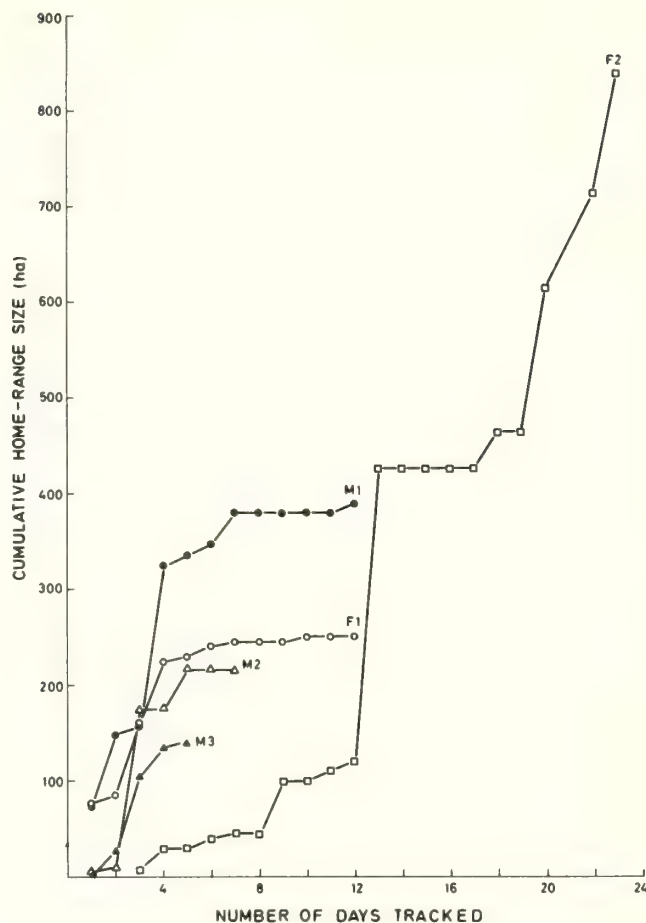


Figure 3. Cumulative home range size for 5 Hawk Owls, as calculated by the convex polygon method, in relation to number of days tracked (M=male, F=female).

There was a positive linear correlation between the quadrate home range size and the number of plotted perching. The quadrate method considers only which parts of the polygon convex home range that are observed being used. Since the use of the different squares within the convex polygon home range is non-random (B.T. Bækken, J.O. Nybo and G.A. Sonerud, unpubl.), the number of squares used will be far less than the number of perching plotted. Hence, with the square-size employed (16 per km²), more than a hundred plotted perching seems necessary in order to obtain a quadrate-based home range covering the convex polygon-based one.

The home ranges of the Hawk Owls were larger when calculated by the convex polygon method than when calculated by the quadrate method. The same difference was found for home ranges of Stone Martens *Martes foina* (Föhrenbach 1984). The convex polygon method should be used to obtain an estimate of the home range size of Hawk Owls, because this estimate is dependent on the number of days tracking, but not on the number of plotted perching. The quadrate method should on the other hand be used when analyzing such topics as

search strategies and habitat selection. Sufficient effort for an accurate estimate during the snow-free season seems to be approximately 10 days, with approximately 10 perchings plotted per day.

ACKNOWLEDGEMENTS

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Observations of the Northern Hawk Owl in Alberta¹

Edgar T. Jones²

Abstract. A discussion of general range and diurnal hunting habits, including observations in the MacKenzie Delta, N.W.T. Canada. An outline is given of observations made during the discovery of four nests indicating nest site variation and feeding habits of both sexes. Dates of nestings for Alberta region are outlined. Winter hunting techniques are discussed, along with encounters with the species using fishing rod and mouse in the early 1960's.

INTRODUCTION

This paper is a collection of my personal observations from the early 1950's to 1974. I discovered my first nest in Flatbush, Alberta, Canada in 1952.

RANGE

The range of this owl in Canada extends across the boreal forest zone from the Yukon and Alaska west to Newfoundland. The breeding range extends north to the treeline and as far south as central Alberta and south-central Ontario. I have seen several Hawk-Owls along the channels of the MacKenzie delta 100 miles inside the Arctic circle. I have also encountered the species at 1700 meters (5500 feet asl) in the dead of winter in Banff National Park.

In winter, the habitat becomes more varied as this bird tends to seek out open areas of parkland where the fields are bordered with small poplar. The fringes of muskeg are a favorite winter/spring haunt, particularly in the latter part of winter when the pairs start to set out their breeding territory. A

larger part of its breeding range is in the area of 24 hour daylight, and the bird is largely diurnal; even in the short days of winter, it hunts during daylight hours.



Figure 1. A hunting Hawk-Owl surveys a grassy muskeg clearing from the top of a black swamp spruce (*picea mariana*) in northern Alberta, Canada.

¹Northern Forest Owl Symposium. February 3-7, 1987. Viscount Gort Hotel, Winnipeg, Manitoba, Canada.

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IDENTIFICATION

Several characteristics quickly differentiate this species from other owls. When hunting, its habit of perching on the tip of the tree rather than half way down or on a lower branch, is very consistent. Even when it is sitting on small poplars or willows, it displays a horizontal stance rather than an upright stance as most owls tend to take. The long tail and its habit of flicking it, in a manner similar to the Kestrel, are two important characteristics. I have seen it hovering on two occasions, another unexpected trait that separates this owl from other species. As for sound, in my association with these birds, I have found them to be very quiet. I have only heard the occasional feed call when I was near the nest site and have never heard any calls while the birds were hunting.

FOOD AND HUNTING TECHNIQUES

During the breeding season, its food generally consists of small mammals such as red-backed and meadow voles, and deer mice. Undoubtedly some small birds are also taken, but certainly in the wintering areas voles and deer mice would be the most likely prey. I would suspect that redpolls, snow buntings and other smaller wintering species would be part of the winter food fare but I have not personally observed this.

They have acute hearing and extremely keen eyesight. On one occasion I watched a Hawk-Owl hunting from the top of a 6 meter (20 feet) black spruce after a deep, soft snowfall. The bird cocked its head to the side several times and then literally dropped off of the spruce into the deep snow. Only the tips of the wings and tail were visible and yet within a few seconds the bird flew up to the tree clutching a vole. This catch was obviously made by sound only as the vole was at least one foot below the snow surface.

In the early 1960's I attracted Hawk-Owls into close range for photography by using a dead mouse as a lure. The mouse was tied to a monofilament line and, with the aid of a spinning rod, cast out onto the snow surface. It soon became evident that a hunting Hawk-Owl could see the mouse up to 730 meters (800 yards) away. The owl would leave its perch and head toward the mouse even before it could be reeled in more than 3 meters (10 feet).

A friend, Bob Gehlert of Edmonton, Canada, developed a technique in the early 1960's which has allowed him to catch and band almost one hundred Hawk-Owls over the last 25 years. His technique simply involved releasing a live house mouse at his feet when a Hawk-Owl was spotted. Within a second or two the owl would head for the mouse. As it came near the mouse he used a fish-landing net to intercept and catch the owl within a meter or so of where he stood. Timing was critical in order to save the mouse for another catch. This demonstrates the incredible fearlessness of this little owl and its concentration on the prey target.

BREEDING AND NESTING AREAS

In north-central Alberta, this bird is considered an early nester. I have found that they are usually on their nesting territory by mid-March and start to lay in mid-April. The following are the dates I have from my nesting records:

April 25, 1952: 6 eggs. This nest was in a burnt out tamarack stump at 6 meters (20 feet). The five young were ready to leave on May 24th.

May 15, 1970: Five young were found feathering out in a nest located in a spruce snag at 6.7 meters (22 feet).

May 17, 1970: We caught and banded the female at a nest which was at 9 meters (30 feet) in a live Balsam Poplar where a branch had broken off leaving a hole. There were seven young between ten to 12 days old. On May 23rd, at this same nest a different adult was caught and banded along with four of the six young remaining in the nest. The two young not banded were too small to retain the band.

June 6, 1975: My associate, Bob Gehlert, found a nest at 4.3 meters (14 feet) in a burnt out spruce stump containing two half-grown young. This nest was in a dense spruce much less open than other locations.

Finding the nest is relatively simple once the breeding territory or the male by himself has been located. By watching the male carefully, when prey has been caught, the male flies directly to the nest so that once this line of flight has been established it is a matter of following it for 90 to 450 meters (100-500 yards) until the nest site is located. The male brings prey to the female on the nest. She may leave briefly to take it from the male either at the nest entrance or a short distance away. If there are young in the nest, the female will return directly to the nest with the food. All this will often be done with an observer close by as the birds have little or no obvious fear of

man.

The nesting site varies with the nests I have observed, but it is usually in or on the fringe of a muskeg. Some sites are in dense Black Spruce, others are in open locations. The most favored location seems to be a burnt out stump with a hole at any height from two to nine meters (8-30 feet). Apparently this species sometimes nests in an old crow's or hawk's nest, but I have never personally observed this. The clutch size varies from three to seven, but usually is five or six.

A word of warning to anyone attempting to climb the nest stump or tree: The Hawk-Owl will not hesitate to attack an intruder.

ENEMIES

Its greatest enemy, without question, is man. The annual destruction of thousands of acres of potential breeding territory, much of which is marginal agricultural land, is the greatest contributing factor to the ever retreating breeding area of the Hawk-Owl, at least in Alberta, Canada.

BANDING RESULTS

Bob Gehlert reports several Hawk-Owls that have been recaught, some from the same tree and several from the same immediate area where the birds were originally banded. I have not received any returns from the ones I have banded.

Foraging Activity and Growth of Nestlings in the Hawk Owl: Adaptive Strategies Under Northern Conditions¹

Kauko Huhtala, Erkki Korpimäki, and Erkki Pulliainen²

Abstract.--Foraging activity was recorded at four nests of the Hawk Owl *Surnia ulula* in C. and N. Finland. The owls brought food to the nest throughout the day, apart from a 2-3 hour pause around midnight. The frequency of nest visits was greatest in early morning (3-4 a.m.), around noon (11 a.m.-1 p.m.) and in late evening (8-11 p.m.). The parent owls visited the nest an average of 10.6 times per day during the incubation period, increasing their visits to 16.6 per day during the hatching period and to 41.4 during the nestling period. They also brought food from the nest to store in its immediate vicinity. The nestlings clearly invested in increasing their body weight at the early stage of the nestling period, the growth of the wings being rather slow. The foraging and growth strategies of the Hawk Owl show adaptation to harsh northern conditions, with continuous daylight, variable food resources and relatively few competitors.

INTRODUCTION

The distribution of nesting Hawk Owls, *Surnia ulula*, is concentrated in the north-boreal zone of the northern hemisphere (for distribution map, see Mikkola 1983) to such an extent that it can be expected that special strategies should have evolved to ensure their success in these adverse and in some respects unpredictable conditions. Because the species also nests in areas characterized by continuous daylight, it has been suggested that it is day-active (Mikkola 1972). Although the hole-nesting Hawk Owl is rather easy to study, surprisingly little is known about its biology, and this is also true of its foraging activity and the growth of its nestlings which we intend to describe in this contribution.

MATERIAL AND METHODS

Visits by the Hawk Owls to four nests were recorded as follows:

1) Direct observations were made from a hide at a nest in Värriö Nature Park (67.5°N, 29.5°E), E. Finnish

Forest Lapland, for two days during the hatching period in 1982. Small rodent populations in that year may be described as "average".

2) Nest visits were recorded by an automatic recorder (type "Norma", see Korpimäki and Huhtala 1986) from the laying period to the end of the nestling period at Ylivieska, (64°N, 24.5°E), W. Central Finland, in 1974. Local small rodents were at their peak in that year.

3) Nest visits were recorded with an automatic recorder during the incubation period (7 days) and hatching period (10 days) at Kauhava, (63°N, 23°E), W. Central Finland, in 1977. This nest was later lost for some unknown reason. Local small rodent populations were at their peak.

4) Nest visits were recorded during the incubation period (8 days) and nestling period (16 days) at Kauhava in 1986. The young in this nest were also weighed on a Pesola spring balance and their wing lengths were measured every other day. A recorder made from a tachograph was used at both nests at Kauhava (see Korpimäki 1981).

RESULTS

The Hawk Owls visited their nests throughout the day, apart from a 2 or 3 hours pause around midnight (figs. 1-3), the length of which was reduced by the need to feed the nestlings (see especially fig. 3). The frequency of the visits varied in periods of 2-3 hours, with peaks in the early morning (3-4 a.m.), around noon (11 a.m.-1 p.m.) and in the late evening (8-11 p.m.) (figs. 1-3). Here again the variation seems to decrease during the nestling period (figs. 1 and 3).

¹Paper presented at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

²Kauko Huhtala is Assistant of Zoology, Erkki Korpimäki is Researcher of the Academy of Finland, and Erkki Pulliainen is Professor of Zoology at the Department of Zoology, University of Oulu, Oulu, Finland.

The need to visit the nest naturally depends on the stage of the breeding process, the number of visits increasing from the incubation period towards the end of the nestling period. The owls visited the nest an average of 10.6 times per day during the incu-

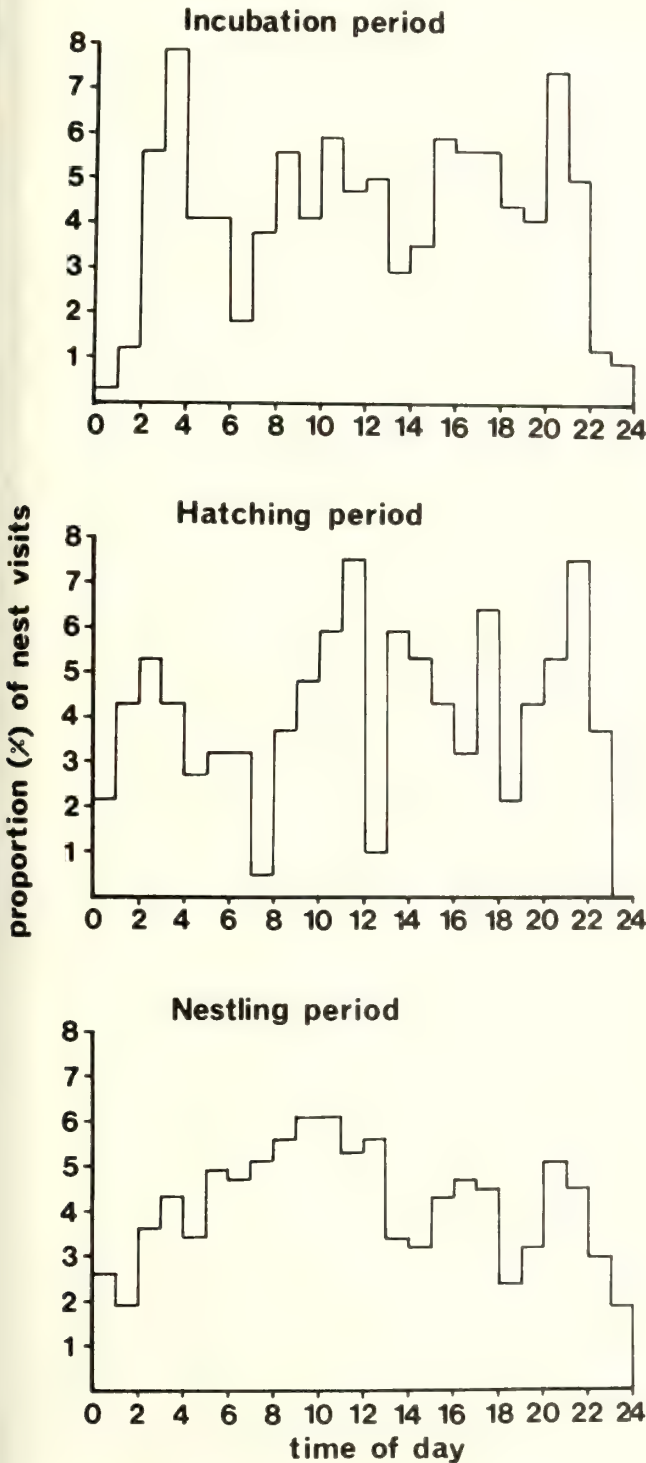


Figure 1.--Diurnal pattern of nest visits of Hawk Owls at Ylivieska in 1974 during the incubation (above), hatching (middle) and nestling periods (below).

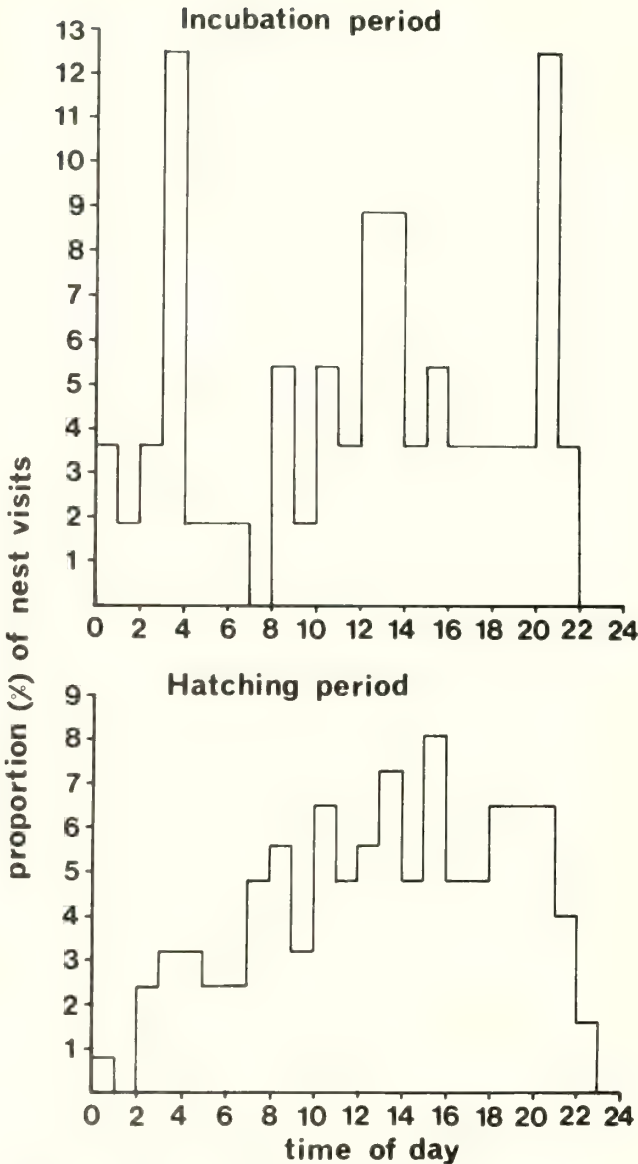


Figure 2.--Diurnal pattern of nest visits by Hawk Owls at Kauhava in 1977 during the incubation (above) and hatching periods (below). The mean number of visits per day was 8.0 ± 1.2 ($N = 7$) during incubation and 12.4 ± 2.2 ($N = 10$) during hatching.

bation period, but not only in order to incubate or bring food, because the observations made in the Värriö Nature Park also suggest that they took food from the nest to nearby cache sites (2-3 times/day by the males). The mean number of visits to the nest increased to 16.6 during the hatching period, and to 41.4 during the nestling period, with a further increase in the course of the nestling period, the number varying between 20 and 30 at first, but between 40 and 50 by the time the young were 16-20 days old. Once the young had passed the stage of rapid weight increase nest visits by their parents decreased (fig. 4). The present data also suggest that there may be some variation between parent birds in this respect

(fig. 1 versus figs. 2-3) which may be due to differences in caching behaviour, in cleaning of the nest, or in the abundance of food available.

The newly hatched young of the Hawk Owl weigh about twice as much as those of its smaller relative, Tengmalm's Owl, *Aegolius funereus*, but their wings are only 2 mm longer (table 1). The nestlings tend to increase in weight very rapidly during the first 2.5 weeks of their lives (fig. 4), an average of 9 g/day, which is three times the rate of Tengmalm's Owl at the same age. In contrast, wing length increases only 1.5 times as much as in Tengmalm's Owl nestlings. The wings of young Hawk Owls grow throughout the nestling period, but their weight gain ceases at the age of 2.5 weeks (fig. 4). They leave the nest at the age of 3-4 weeks, having achieved 78 % of the weight of their parents, but only 60 % of their parents' wing length (table 1). In the case of Tengmalm's Owl the situation is different when leaving the nest, at the

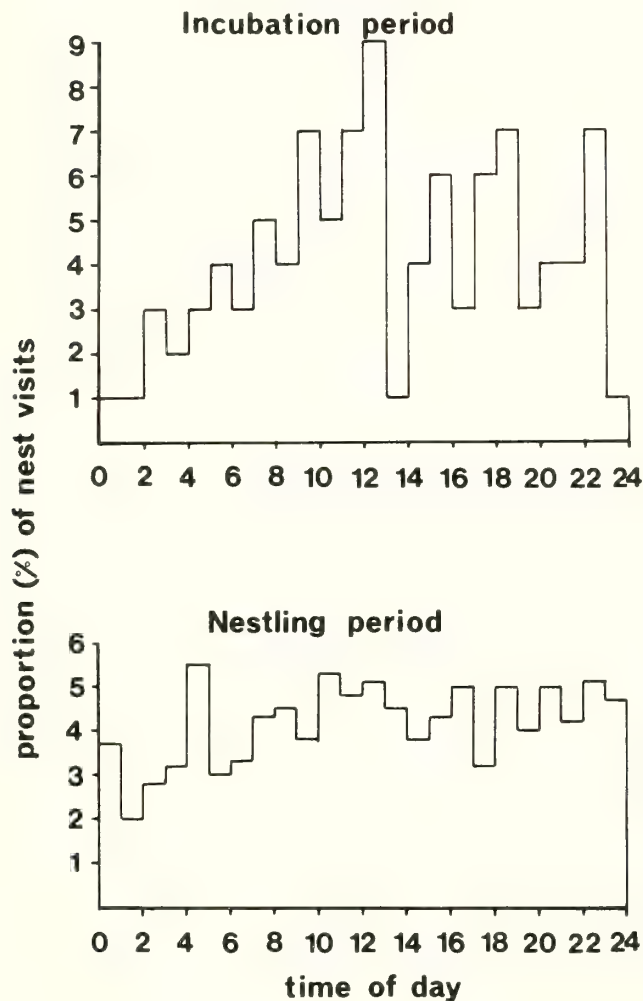


Figure 3.--Diurnal pattern of nest visits by Hawk Owls at Kauhava in 1986 during the incubation (above) and nestling periods (below). The mean number of visits per day was 10.8 ± 2.7 ($N = 8$) during incubation and 37.7 ± 7.3 ($N = 16$) during the nestling period.

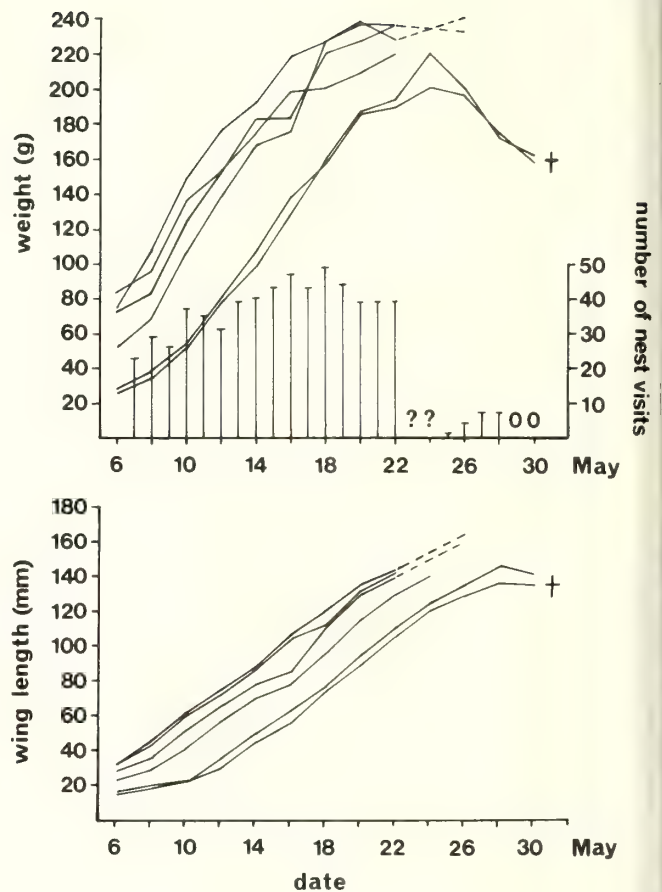


Figure 4.--Weight gain (above) and wing growth (below) in Hawk Owl nestlings compared with the number of daily nest visits by the parent owls (above, columns) at Kauhava in 1986. The cross denotes a young that died in the nest. ? = recorder was not functioning, 0 = no visits to the nest.

age of 4.5 weeks. The young are able to fly, their weight is 91 % of that of their parents and their wing length is 71 % of that of their parents (table 1).

DISCUSSION

An automatic recorder installed at an owl's nest does not tell what kind the visit has been recorded, since feeding trips leave similar marks to trips when the owl carries away food remains or pellets. Female owls also defecate outside the nest, so that a female Great Grey Owl, *Strix nebulosa*, for instance, leaves the nest 3.1 times/day on average during the incubation period and 3.7 times/day during the nestling period (Pulliainen and Loisa 1977). The corresponding figure for Tengmalm's Owl is 2.1/day (Korpimäki 1981). A female Hawk Owl eats the pellets produced by the nestlings during the hatching period (Leinonen 1978). The direct observations made in the Värriö Nature Park comprised only feeding or caching events,

Table 1.--Growth of nestlings of the Hawk Owl compared with that of nestlings of the Tengmalm's Owl. Sources in parentheses.

	Hawk Owl		Tengmalm's Owl	
Weight of adults (g, mean of female and male)	295	(1)	134	(2)
Wing length of adults (mm, mean of female and male)	236	(1)	173	(2)
Mean nestling period (days)	23	(3)	32	(2)
Mean weight of young (g)				
at hatching	18	(3)	9	(2)
at fledging	230	(3)	122	(2)
Mean weight gain of nestlings per day (g)	9.2	(3)	3.5	(2)
Weight of fledglings as % of adult weight	77.9	(3)	91.2	(2)
Mean wing length (mm)				
at hatching	13	(3)	11	(2)
at fledging	141	(3)	124	(2)
Mean wing growth of nestlings per day (mm)	5.6	(3)	3.5	(2)
Wing length of fledglings as % of that of adults	59.7	(3)	71.7	(2)

Sources: (1) Mikkola (1983), (2) Korpimäki (1981) and unpubl., and (3) this study.

which means that the activity recorded mainly describes the feeding by the parent owls.

It can be expected that a bird of prey, such as the Hawk Owl, which mainly feeds on small rodents in the continuous daylight and unpredictable conditions of the north, develops a strategy which takes full benefit of this daylight period for catching its prey and for ensuring that the nestlings grow as rapidly as possible. When the decision to breed has been made by the parents on the basis of the local small rodent population, it is important to use this natural resource as rapidly as possible, since there are other simultaneous users of the same resource.

The present data show that Hawk Owls made efficient use of the long daylight period for catching prey and feeding their nestlings (figs. 1-3). They also collect small rodents to store nearby, to be available for intensive feeding of the young. This efficiency is reflected in the clutch size and general productivity of the species as compared with other owl species of the north-boreal zone (data from Mikkola 1983). This result is the product of hard work, however, as the Hawk Owl visits its nest 3-4 times more often than any of the other north-boreal owls; Tengmalm's Owl doing so 8.3 times/day during the nestling period (Korpimäki 1981), the Ural Owl *Strix uralensis* 13.0 times/day (Korpimäki and Huhtala 1986) and the Great Grey Owl 9.7 times/day (Pulliainen and Loisa 1977).

The northern owls (e.g. *Strix nebulosa*, *Nyctea scandiaca* and *Surnia ulula*) are in general day-active, which is natural, since there is continuous or almost

continuous daylight during most of their breeding season. This may be in contradiction to the optimal foraging theory (see Pyke et al. 1977), because the small rodents show "night-activity" in the spring (for *Clethrionomys* spp., see Pearson 1962, Bergstedt 1965, Mikkola 1970; for *Microtus* spp., see Erkinaro 1969), but the reality of continuous or almost continuous daylight obviously forces the owls to use this time for hunting, and the present data confirm that enough prey is available throughout the day. On the other hand, the number of other day-active birds of prey eating small rodents in the north-boreal zone is low (primarily *Buteo lagopus* and *Stercorarius longicaudus*), which reduces competition as compared with the situation in more southerly areas.

In fact the Hawk Owl appears to hunt when small rodents are available and gather extra prey into stores in the vicinity of the nest (also Leinonen 1978, Ritchie 1980). This allows them to feed their nestlings continuously, providing for rapid growth. On the other hand, the Hawk Owl faces technical problems in this storage process, for the species favours nest holes which are shallow (K. Huhtala, unpubl. data), and these cannot be used as storage sites like those of Tengmalm's Owl are (Korpimäki 1981). The clutch of the Hawk Owl is also larger than that of Tengmalm's Owl, which again detracts from this strategy. But there is also some benefit from a shallow nest hole, since the incubating female may watch over the prey stored in the trees nearby and defend them against robbing by for example corvids (see Thönen 1965). Prey stores are probably a buffer against temporary food shortage caused by, for example, heavy snowfalls. In the breeding season, weather conditions may suddenly deteriorate, for heavy snowfalls may occur in Finnish Forest Lapland up to the beginning of July (Pulliainen 1978). Ritchie (1980) assumed that the establishment of caches may provide a key to more efficient division of duties between female and male, and may also reduce potential conflicts of parents at the nest. If these were the main points, this kind of cache behaviour would have developed in all the owl species and would not be confined to the northern owls (see also Korpimäki, in press).

Due to limited space in the nest hole, it is reasonable that the young of the Hawk Owl leave their nest as early as possible. A growing young can invest its energy mainly in body weight or wing growth, or in both simultaneously. The Hawk Owl has selected the first alternative, which could be called the "oilbird (*Steatornis caripensis*) strategy" or "fat-young strategy". They leave the nest at the age of only 3-4 weeks, when they are still unable to fly, but they are skilful climbers and their mother continues to watch over them. This strategy is also safe in that there are relatively few potential enemies in their breeding habitats in the north. This "fat-young strategy" also allows some fasting periods during the fledging period, which may be adaptive in these harsh conditions. This, together with the caches of prey animals, provides the young of the Hawk Owl with some measure of life insurance.

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Sexual Size Dimorphism and Life-History Traits of Tengmalm's Owl: A Review¹

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Abstract.--The ecology of Tengmalm's Owl was studied for 21 years in western Finland. At the beginning of the nestling period, females are on average 43 % heavier than males, but their wings are only 5 % longer than those of males. The degree of sexual dimorphism in weight is higher than that of other European owls. Large females have more striking force and catch more voles, whereas small males can also take more agile prey, such as birds. Because of sexual size dimorphism, scarcity of nest-holes and vole cycles, a majority of males is resident but females nomadic in western Finland. Thus, local population fluctuations of females seem to be more pronounced than those of males. Females usually enter the breeding population as yearlings, whereas males only when they are 2-year-old. These intersexual differences in life-history traits suggest that females may be more r-selected than males.

INTRODUCTION

The ecology of Tengmalm's Owl (Boreal Owl in North America) *Aegolius funereus* was studied during 1966-86 in South Ostrobothnia (63°N, 23°E), western Finland. Methods were described in other papers (e.g. Korpimäki 1981, 1983, 1984, 1985a, 1986a, 1987a, b). This paper gives a review of results and also summarizes some other European studies on this species. The main purpose is to compare the life-history traits of female and male Tengmalm's Owls, because the sexes show size dimorphism, with females being markedly larger than males.

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DIVISION OF DUTIES BETWEEN SEXES

Both the incubation and nestling period of Tengmalm's Owl take approx. 30 days (Korpimäki 1981), and thereafter fledglings are fed by mates for at least three weeks (März 1968). As other birds of prey, male and female divide duties in the breeding season. The male provides nearly all food for the whole family from before the egg-laying until the young are three weeks old, but he does not take part in incubating the eggs or brooding the young (Korpimäki 1981).

The female stays in nest-hole from one week before the start of egg-laying until the young are three weeks old, and is entirely fed by the male. So she is responsible for producing and incubating the eggs and for brooding the young. At the end of the nestling period, she takes part in feeding, but only at a low rate (Korpimäki 1981).

SEXUAL SIZE DIMORPHISM

At the beginning of the nestling period, female Tengmalm's Owls are on average 43 % heavier than males, but their wings are only 5 % longer than those of

males (Korpimäki 1986b). The degree of sexual dimorphism in weight is higher than that of other European owls (Lundberg 1986).

Until now, no fewer than at least 20 hypotheses have been advanced to explain the reversed sexual size dimorphism in birds of prey. Lundberg (1986), after analysing size dimorphism in European owls, suggested, that female owls are larger than males in order to reduce the effects of temporary food shortage during the breeding period. This "starvation hypothesis" yields at least six predictions (Korpimäki 1986b, Lundberg 1986): (1) northern species should be more dimorphic in weight than southern ones, (2) earlier breeding species at a given latitude should be more dimorphic, (3) female size and (4) the degree of dimorphism should increase with food unpredictability at breeding, (5) pairs laying early in the season, under unpredictable weather and food conditions, should be more dimorphic, and (6) have larger females, than those laying later, when environmental conditions are more constant.

Lundberg (1986) showed that the prediction 1 was true in European owls. In western Finland, early-breeding species in two communities of vole-eating birds of prey were more dimorphic in weight than late-breeding ones, with Tengmalm's Owl being the earliest-breeding and most weight dimorphic species (Korpimäki 1986b). This is consistent with the prediction 2. The degree of weight dimorphism between mates within pairs of Tengmalm's Owl correlated negatively with the timing of egg-laying, while the wing length of males correlated positively with the laying date of their partners. Clutch size and number of fledglings produced decreased with the degree of weight dimorphism within owl pairs (Korpimäki 1986b). These results are in agreement with the predictions 5 and 6.

Because of clear division of duties in the breeding season, different selective factors act on females and males. It seems that the large size of female Tengmalm's Owls has evolved in order to increase their fasting endurance. Food items are delivered to the female by the male at long and unpredictable intervals, because breeding starts at the end of March or at the beginning of April under adverse weather conditions. At that time, usually occurring snowfalls decrease the hunting success of the male (Korpimäki 1987c). In contrast, selection acts on males to become efficient foragers. Aerial agility increases with decreasing wing length (Andersson and Norberg 1981). Thus,

Table 1.--Number of available nest-boxes or holes, number of Tengmalm's Owl nests, percentage of nest-holes used, number of unpaired males, and number of nests in which parent owls were trapped during 1979-86 in western Finland.

Year	Number of holes	Number of nests (1)	Per cent used	Number of unpaired males (2)	Number of nests in which parent owls were trapped (3)	Females Males
1979	355	37	10.4	6	31	14
1980	395	24	6.1	16	24	9
1981	395	10	2.5	18	7	6
1982	415	34	8.2	18	34	25
1983	450	27	6.0	30	25	19
1984	450	10	2.2	4	10	7
1985	450	47	10.4	11	35	36
1986	450	88	19.6	15	81	76
Tot.	3360	277	8.2	118	247	192

Note. (1) See Korpimäki (1981, 1984, 1985a, 1986a, 1987a, b) for methods used in collecting data on population fluctuations and breeding performance.

(2) In late February and March (i.e. before the breeding season) nest-sites occupied by male Tengmalm's Owls were localized by listening to displays, using the point-stop method and playback technique (e.g. Lundberg 1978, Holmberg 1979). Later checking visits to nest-holes revealed the males, which were stayed unpaired.

(3) See Korpimäki (1981, 1983, 1987a) for trapping methods.

small males probably are more effective and economical hunters and better competitors for good territories and nest-holes (Korpimäki 1986b). In conclusion, the "starvation hypothesis" seems to explain the high degree of reversed size dimorphism in Tengmalm's Owl.

Olsen and Olsen (1984) suggested that reversed size dimorphism of birds of prey might be explained by "sexual selection" (as first outlined by Darwin 1871); namely that competition between females for the more scarce resource, the males, selects for large females. Males may be the more scarce resource, because they hold territories with good nest-site and food supply. This explanation seems to hold true for the European Sparrowhawk *Accipiter nisus* in Scotland (Newton 1986). The sex ratio of this raptor is biased in favour of females, because they are longer-lived than males. In contrast,

there is generally a surplus of males in Tengmalm's Owl populations, probably because of larger mortality of females in comparison to males (Korpimäki et al. 1987). For instance, on average 30 % of males in western Finland were unpaired during 1979-86 (table 1). The most probable reason is a lack of females, because a majority of these males occupied territories, which had earlier been suitable for breeding and where a nest-box was available. Thus, male Tengmalm's Owls may compete for the scarce resource, the females. So it seems that the high degree of sexual dimorphism of this owl cannot be explained by "sexual selection", but only further studies will show, which factors are most important.

HUNTING HABITS

Male Tengmalm's Owls have a wider prey spectrum than females; females catch more voles, whereas males take more birds (Korpimäki 1987d). These differences may be caused by the following factors. (1) Small, nimble males are better adapted to catch birds, which are very agile prey. (2) Large females have more striking force and are therefore better suited for hunting relatively large voles, such as *Microtus* spp. in Fennoscandia. (3) Agile males may more often hunt in forest and "clumsy" females in open ground. (4) Females have smaller wing-load in relation to their body weight than males; so they may more often perch when hunting, whereas males may more often quarter. Perching is more suitable for catching small mammals and quartering for capturing birds. However, these explanations are only suggestions, because there are no data on possible differences in prey preference, and hunting habitats or habits between female and male Tengmalm's Owls. The former should be studied experimentally in captivity and the latter by radio-tracking in autumn or winter, when both sexes hunt only for themselves.

WINTERING STRATEGIES

Tengmalm's Owl is a hole-nester, which suffers from a scarcity of nest-sites at least in Fennoscandian coniferous forests (von Haartman 1968, Lundberg 1979). Site-tenacious owls benefit by familiarity with local food resources, refuges from predators and nest-sites (Hinde 1956, Korpimäki 1987a). Both a scarcity of nest-sites and familiarity with territories favour residency.

Tengmalm's Owl uses small rodents, mainly voles, as its staple food. The most important alternative prey groups are

shrews and birds (Sulkava and Sulkava 1971, Korpimäki 1981, 1986c). Vole populations are relatively stable in central Europe, but show 3-5-year cycles in Fennoscandia, with most pronounced fluctuations in the north and least pronounced in the south (Hansson and Henttonen 1985). However, abundances of voles in various areas fluctuate asynchronously (e.g. Myllymäki et al. 1977); so this cyclical food production favours adult nomadism (Andersson 1980). Because of its small body size, Tengmalm's Owl cannot hunt effectively small rodents protected by deep snow layer (Korpimäki 1987d). In general, the persistence and depth of snow cover increase northwards in Fennoscandia, although the snow layer in southern and western Finland is much shallower than at the same latitudes in eastern Finland and Sweden. Thus, it would be adaptive for Tengmalm's Owls to overwinter in areas of shallow snow cover.

The above-mentioned opposite selective pressures result in differences in breeding dispersal (*sensu* Greenwood and Harvey 1982) between the sexes: (1) Probably all males and a majority of females are resident in central Europe, (2) a majority of males is resident but a majority of females nomadic in the transition zone (e.g. in southern and western Finland), and (3) many males are also nomadic in northern Fennoscandia (Korpimäki 1986a, Löfgren et al. 1986). According to Korpimäki et al. (1987), the similar intersexual differences are also evident in the natal dispersal (*sensu* Greenwood and Harvey 1982).

The resident habit of male has been suggested to have evolved to ensure access to nest-holes, which are in short supply (Lundberg 1979). Thus, males must guard their nest-holes against competitors also outside the breeding season. Agile males are better able to hunt alternative prey and in forest than "clumsy" females. The availability of small mammals and birds in winter is better in forests than in open ground (Korpimäki 1986c). Because the male is responsible for food provision in the breeding season, he benefits by the detailed knowledge of the territory. Resident males can better compete for a scarce resource, females, and thus their partners lay earlier and larger clutches than those of immigrant males (Korpimäki 1987a). These factors may further favour the residency of males.

Females are more specialized to prey on small rodents than are males, and thus they willingly overwinter in areas of high abundance of voles and shallow snow cover. They benefit by familiarity with the territory only during a short time period

at the end of the nestling period. These reasons may explain, why females are nomadic.

LIFE-HISTORY TRAITS OF FEMALES AND MALES

The life-history of any species is made up of a complex of adaptive traits (Stearns 1976, 1977), but there may also be intraspecific differences in life-history traits (Stearns 1980). The model of *r*- and *K*-selection is often used to explain life-history phenomena, although its importance for our understanding of life-history evolution has generated also some controversy in recent years (Boyce 1984).

Stearns (1976) summarized the environmental and organismic correlates of *r*- and *K*-selection. *r*-selection is characterized by, e.g. a variable population size in time, early reproduction and short lifespan. In contrast, *K*-selection is outlined by, e.g. a constant population size in time, delayed reproduction, keen competition and long lifespan.

Table 2.--Number (N) and percentage (%) of female and male Tengmalm's Owls belonging to the three age classes when making their first breeding attempt within the study area in western Finland. Pooled data from 1985-86.

Age class	Females		Males	
	N	%	N	%
1 yr	53	53.0	17	22.4
2 yr	22	22.0	39	51.3
+2 yr	25	25.0	20	26.3
Total	100	100.0	76	100.0

Note. (1) From 1981 onwards at least 60 % and from 1982 onwards at least 70 % of breeding females and males were trapped and ringed (see table 1). All fledglings in known nests were ringed during 1973-86. So one could identify which owls were recruits in the breeding population.

(2) First-year and second-year owls were differentiated from older ones by checking the moult score of primaries according to Glutz von Blotzheim and Bauer (1980). The reliability of this method was confirmed by 27 retrapped known-age owls (E. Korpimäki unpubl.).

Suggesting that there are no non-breeding females in the population, the number of females varied between 10 and 88

(mean 34.6 ± 25.0) and the number of males between 14 and 94 (mean 47.6 ± 23.6) during 1979-86 in South Ostrobothnia (table 1). The coefficient of variation ($CV = 100 \times S.D. / \text{mean}$) for females (72 %) is markedly larger than that for males (50 %). Thus, the number of males seems to be more constant than that of females, but only further studies will show, whether the population also includes some non-breeding females.

Assuming that the probability of the first breeding attempt occurring within the study area is similar for both sexes, females start to reproduce as significantly younger than do males (Mann-Whitney U-test, two-tailed; $U = 4696.5$, $P < 0.01$; table 2). Females usually enter the breeding population as yearlings, whereas males only when they are 2-year-old. Males compete for females, and territories with good nest-hole and food supply, but females can usually make a choice between several males and territories, because there are many unpaired males in the population (table 1). This biased sex ratio in favour of males is probably caused by the higher mortality of females during irruptions (Korpimäki et al. 1987) and by Pine Martens *Martes martes*, which sometimes kill females in their nest-holes (e.g. Korpimäki 1981, Sonerud 1985). Thus, males seem to be longer-lived than females.

In conclusion, the present results suggest that there are marked differences in the life-history traits of female and male Tengmalm's Owls; females seem to be more *r*-selected than males. This coincides with the *r*-selected nature of females' main prey (i.e. voles) and allows the breeding population to respond rapidly to the population fluctuations of voles, because of immigration of females to good vole areas (Korpimäki 1985b).

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Annual, Seasonal, and Nightly Variation in Calling Activity of Boreal and Northern Saw-Whet Owls¹

David A. Palmer²

Abstract.-- Calling activity of Boreal and Northern Saw-whet Owls was monitored over a 6-year (1980-1985) period in north-central Colorado. Intensive surveys were completed in 1983 and 1984 to determine nightly variations in calling intensity and to assess the influence of environmental conditions on calling activity. Calling activity of both species fluctuated considerably over the 6-year period and appeared to be associated with changes in owl prey populations. Both species reached peak calling activity in 1984 when 14 saw-whet and 27 boreal owls were heard. Overall length of the courtship period ranged from 31 to 119 days (avg. = 63) for boreal owls and from 70 to 93 days (avg. = 81.5) for saw-whet owls. Calling activity of boreal owls was slightly influenced by wind, precipitation and moon phase while cloud cover and temperature had no apparent effect. Saw-whet owl calling activity was influenced by wind and slightly by moon phase.

INTRODUCTION

Both the Boreal Owl (*Aegolius funereus richardsonii*) and the Northern Saw-whet Owl (*A. acadicus*) are small, nocturnal owls which have wide distributions in the northern regions of North America (Burton 1977, AOU 1983). Because of their small size, secretive habits and generally northern range, the owls' biologies are poorly understood, especially regarding habitat requirements and breeding biology. Although generally secretive, both species are extremely vocal during the early breeding season and can be located with relatively little effort using nocturnal surveys (Holmberg 1979, Webb 1982). Kuhk (1953) considered Tengmalm's owl (*A. f. funereus*), one of the European subspecies of the boreal owl, to be one of the most persistent singers among European owls and found the males easy to locate for a brief period in the spring. Information on calling activity of boreal owls in North America is limited to the behavioral significance of vocalizations (Bondrup-Nielsen 1978, 1984, Meehan 1980) while little is known about any facet of saw-whet owl calling activity.

Nocturnal surveys have been used to estimate Tengmalm's owl populations in Europe (Lundberg 1978, Holmberg 1979) and recently to locate breeding boreal owls well south of their previously recognized breeding range (Eckert and Savaloja 1979, Hayward and Garton 1983, Palmer and Ryder 1984). Webb (1982) used nocturnal surveys to determine the populations status of five species of montane owls, including boreal and saw-whet owls in the Colorado mountains. Nocturnal surveys can be utilized to determine habitat preferences, population densities and fluctuations, and to aid in nest location. Nocturnal surveys, utilizing both road counts of calling owls and elicitation of owl calls using playback recordings, have been used extensively to determine the status of several owl species in North America (Call 1978, Fuller and Mosher 1981, Johnson et al. 1981). In this study, boreal and saw-whet owl calling activity was monitored over a 6-year period (1980-85) in northern Colorado to determine how calling activity fluctuates on an annual, seasonal and nightly basis. Additionally, information was collected to determine how various environmental conditions influence the calling activity of both owl species.

STUDY AREA AND METHODS

The study area, located in western Larimer and eastern Jackson counties in north-central Colorado, ranged in elevation from 2370 to 3300 m. The higher elevation areas were covered by spruce-fir (*Picea engelmannii*-*Abies lasiocarpa*) and

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lodgepole pine (*Pinus contorta*) forests while Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) forests predominated at lower elevations. Trembling aspen (*Populus tremuloides*) was common in riparian areas at lower elevations.

Both species of owls have a wide repertoire of vocalizations (Johnson et al. 1979, Karalus and Eckert 1979, Bondrup-Nielsen 1984) but only the primary, or mate attraction, calls were used for the purposes of this investigation. Male boreal owls render the primary vocalization from late winter until pair formation or until the season has progressed past the point where nesting is feasible (Bondrup-Nielsen 1984) while male saw-whet owls call more softly and less frequently after pair formation (pers. obs.). Both species call occasionally in the fall (Kuhk 1953, pers. obs.).

Owl calling activity was monitored using a modification of the aural census method described by Holmberg (1979). While driving, I stopped and listened for vocalizations for 5 to 10 minutes every 0.7 km along 57 km of roads within the study area. Nocturnal surveys were conducted at least once every 2 weeks from April through June 1980 and January through June 1981-1985. Tape recordings of the species' primary vocalizations were used in 1981, 1982 and 1985 to elicit calls.

Intensive surveying was done in 1983 and 1984 during which time surveys were conducted almost every night. During this period, censuses were started at dusk and usually ended by 0200. Early morning censuses, begun at 0200 and ending at dawn, were conducted periodically throughout the study period. Starting locations were alternated on a nightly basis so that all areas were sampled at different times of the night. Approximately 75% of the study area was composed of habitat occupied primarily by boreal owls while 25% was occupied by saw-whet owl habitat so that the amount of time spent censusing boreal owls was more than that spent on saw-whet owls. Censuses were not conducted on nights with extremely heavy snowfall or high winds. Each time an owl was heard during this period (1983-84) I recorded the following variables: temperature; wind speed (Beaufort scale) and direction; degree of precipitation (0-3); percent cloud cover (0-4); the phase of the moon (new, 1/4, 1/2, 3/4, and full) and degree of illumination (0-4), from no moon, or a moon completely occluded by clouds, to a full moon with a clear sky. Tape recordings were used occasionally to try to capture the owls but were not used to elicit calling.

RESULTS AND DISCUSSION

The primary emphasis from 1980-82 was placed on locating boreal owls only; and only a portion of lower elevation habitat types, where saw-whet owls were most numerous, was sampled during this period. Census routes were completed 130 times in habitat types occupied by boreal owls and 94 times

Table 1. -- Results of aural censuses for boreal and saw-whet owls from 1980 to 1985 in Larimer and Jackson counties, Colorado.

Year	# census	#boreal	Owl species		
			#/hr	#saw-whet	#/hr
1980	10	5	0.50	*	
1981	10	8	0.42	3	0.50
1982	11	3	0.27	0	0.00
1983	44	9	0.15	2	0.11
1984	45	27	1.13	14	1.43
1985	10	0	0.00	1	0.10

*no attempts were made to locate saw-whet owls in 1980.

in habitats where saw-whet owls were found, from April 1980 to June 1985 (table 1). At least one boreal owl was heard on 64 censuses (49%) while saw-whet owls were heard less frequently (30 censuses or 32%). Saw-whet owls were heard at elevations ranging from 2370 to 2700 m in primarily deciduous riparian areas while all boreal owls were located in coniferous forests above 2770 m. Because of the amount of variation in censusing effort from year to year, all owl numbers are presented as both total numbers and owls per hour of census.

Annual Variation

Fifty-two boreal and 18 saw-whet owls were heard calling during the period. The number of boreals ranged from 0 (0/hr) in 1985 to 27 (1.13/hr) in 1984, while numbers of saw-whets ranged from 0 (0/hr) in 1982 to 14 (1.43/hr) in 1984 (table 1). A high degree of annual variation in the number of individual owls found calling has been widely reported for boreal and Tengmalm's owls and is usually associated with fluctuations in small mammal populations (Lundin 1961, Lundberg 1978, 1979, Bondrup-Nielsen 1978, Korpimäki 1981, 1985). In years when small mammal populations are depressed, owls may be present but choose not to call because of the unlikely chance of breeding successfully (Lundberg 1979).

Small mammal trapping on the study area from 1983 to 1985 revealed that red-backed voles (*Clethrionomys gapperi*) and *Microtus* spp., the boreal owl's principal prey on the study area, increased significantly from 1983 to 1984 and then decreased in 1985 (table 2). Deer mice (*Peromyscus maniculatus*) decreased from 1983 to 1984 and again in 1985. Boreal and saw-whet owl calling activity was correlated with population trends of *Clethrionomys* and *Microtus* but not with *Peromyscus* (table 2). A longer term study with a greater sample size is needed to verify this trend but it does agree with what has been found by other investigators.

Table 2.--Results of small mammal trapping during the three years that intensive owl surveys were conducted.

Year	Small mammal capture rates (#/100 trap nights)			
	Deer Mouse	Red-backed Vole	Microtus spp.	Total
1983	2.5	0.4	0.2	3.1
1984	1.8	1.2	0.5	3.5
1985	0.0	0.0	0.0	0.0

Seasonal Variation

The earliest date that boreal owls were heard during the breeding season (January-June) was on 18 February 1984 and the latest was on 21 June 1984 while the earliest and latest dates that saw-whets were heard calling were 29 January and 30 April 1983. The onset of calling for the season was latest for both species in 1981 when boreal owls were first heard on 18 April and saw-whet owls were first heard on 23 April (fig. 1). While saw-whet owl calling had ceased by late April, boreal owls had a lull period in early May followed by an increase in activity in late May-early June (fig. 2). This same pattern was observed for Tengmalm's owls by Kuhk (1953) and Schelper (1972) in West Germany and can probably be attributed to increased activity by males nesting for the first time (Kuhk 1953) or by unpaired males just before

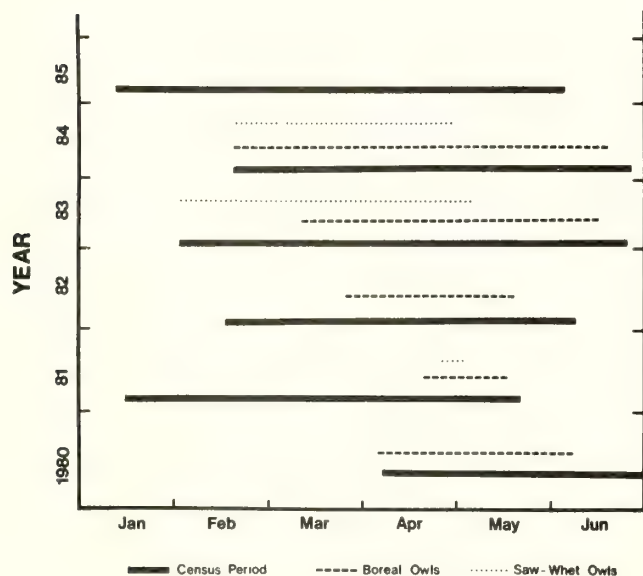


Fig. 1. Duration of the courtship periods of boreal and saw-whet owls, 1980-85, in north-central Colorado.

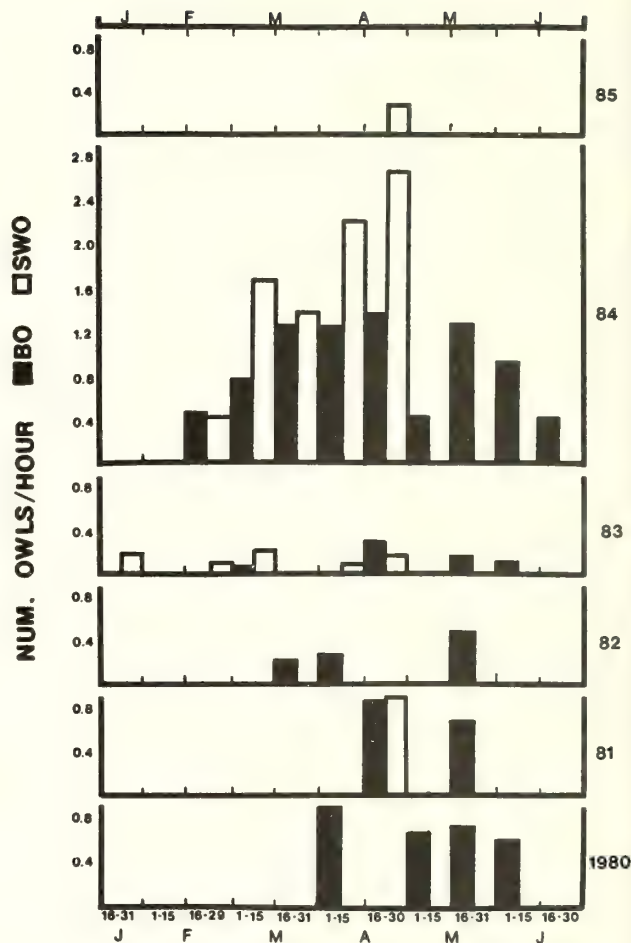


Fig. 2. Distribution of the calling activity of boreal and saw-whet owls during the spring, 1980-85, in north-central Colorado.

they stop calling for the season (Bondrup-Nielsen 1978). Kuhk (1953), Kallander (1959), and Lundin (1961) all report that Tengmalm's owls can be heard in every month of the year except July. I heard no calling in the fall for either species but it has been reported for my Colorado study area (Reddall 1985).

Both the onset of calling and the peak calling period (usually late April) that I found are slightly later than reported for saw-whet owls (Farbotnik 1977-78, Karalus and Eckert 1979). Kuhk (1953), Kallander (1959), Bondrup-Nielsen (1978) and Meehan (1980) all report boreal (Tengmalm's) owl peak calling in late March or early April, about three weeks earlier than the peak that I observed. Holmberg (1979) found that Tengmalm's owl calling activity began earlier and was more frequent in years of high prey populations, possibly explaining the earlier calling dates that I observed in 1984.

Korpimäki (1981) stated that day length is the primary factor regulating the timing of Teng-

Tengmalm's owl breeding in moderate climates, while temperature and food have lesser effects. All of the previous studies of boreal (Tengmalm's) owls mentioned were located at between 55 and 65 degrees north latitude where day length in late March-early April, (approximately 14 h), when peak boreal owl calling occurs, is approximately the same as day length in my study area (40° N) in late April, the period when I found peak calling activity. It appears that day length may regulate breeding in Colorado as well.

According to Bondrup-Nielsen (1978) the courtship period for boreal owls ended at about the same time that the nightly minimum temperature remained above 0 C and the snow was gone from the ground. These conditions were not met on my study area until early summer, precluding these as factors in the timing of the breeding season on my study area. Nightly minimum temperatures when the courtship period ended during my investigation usually ranged between -10 and -5 C. Korpimäki (1981) stated that egg laying can occur with temperatures as low as -20 C if sufficient prey are available to maintain the incubating female's body temperature. Snow depth reached its maximum at about the same time that boreal owl courtship period was at its peak (table 3), indicating that snow depth probably does not play a role in the timing of the breeding season in the high elevations of the Rocky Mountains. Saw-whet owls were found calling at lower elevations where snowfall was less and temperatures were higher, more approximating other areas where they are found breeding, and the timing of their breeding corresponds with breeding in other areas (Santee and Granfield 1939, Johns and Johns 1978, Follen 1981, Norton and Holt 1981).

The duration of the boreal owl courtship period (all owls) ranged from 31 days in 1981 to 119 days in 1984 while saw-whet courtship lasted from 70 to 93 days, excluding 1981 when little effort was expended locating saw-whet owls and they were heard for a period of only five days (fig. 1). Average courtship period for individual boreal owls, excluding those owls heard on only one occasion, ranged from 18.6 days in 1983 to 49.3 days in 1984. The longest courtship period for an individual boreal owl lasted 102 days for

an owl that was apparently unpaired. Saw-whet owls, while not heard in two of the six years (1980 and 1982) and heard only briefly in two others (5 days in 1981 and 1 day in 1985), had approximately the same length courtship period as boreal owls in the two years that they were heard regularly. The longest courtship period of an individual saw-whet was 93 days and it nested successfully.

Bondrup-Nielsen (1978) found average boreal owl courtship periods ranging from 8.2 to 10.2 days while overall courtship length lasted from 28 to 55 days, shorter than the courtship periods that I found. Meehan (1980) found that mated boreal owls have longer courtship periods (average 37.8, days, range 20-51 days) than those that failed to attract mates (range 6-35 days). I was only able to locate four nests during my study and the courtship periods of these successful males ranged from 4 to 59 days (average 26). Throughout my study, however, the owls that had the longest courtship periods were found to be unsuccessful males which sang well into June.

I could find only one reference to the length of a saw-whet courtship period and this was approximately 25 days (Farbotnik 1977-78). Less is known about the saw-whet owl primary call and references made to calling owls in the literature could include a variety of different calls, therefore the duration of the courtship period is difficult to ascertain from the accounts given.

Singing Activity Through the Night

The majority of censuses were conducted between dusk and 0200 with only infrequent surveys from 0200 to dawn. Both species generally began calling within one hour after sunset and sang throughout the census period. Saw-whet owls were heard calling during the early morning censuses more frequently than boreals and they were heard calling in the predawn hours throughout the study period, whereas boreal owls were heard calling in the morning only in the latter half of the study period. Marz (1968) reported that Tengmalm's owls often call for a time after dusk, become silent until midnight, then resume calling until early morning. Meehan (1980) found that boreal owls begin calling after dusk and end by midnight, with few exceptions. I found that once the owls began calling in the evening, for either species, it generally continued until well after midnight with no detectable decrease in intensity.

Table 3.--Snow depth (cm) at the time courtship began and ended for boreal and saw-whet owls from 1980-1985 in northern Colorado.

Year	boreal owl		saw-whet owl	
	first	last	first	last
1980	213	117	-	-
1981	140	61	56	56
1982	180	214	-	-
1983	147	122	11	0
1984	175	122	0	0
1985	-	-	-	-

The Influence Of Environmental Factors On Calling Activity

Several environmental factors which may influence the calling activity of boreal and saw-whet owls were investigated. Because of the relatively few contacts of both species in 1983, I used only data gathered in 1984, when significantly more owls were heard. Analysis of the effects of weather is particularly difficult because

weather variables are often intercorrelated and also correlate with the time of year, habitat and time of night. Armstrong (1963) states that extreme weather conditions tend to inhibit calling, especially early in the courtship period, but as the season progresses birds are less affected. Therefore, owls calling latest in the season may be less likely to be influenced by weather conditions than those that are heard early in the season. In this paper I have treated each environmental variable independently although a combination of factors could have resulted in changes in calling activity of the owls.

Temperature

Low temperatures seemed to have little influence on calling activity of either species once the breeding season began. Boreal owls were heard calling when temperatures were as low as -18 C and saw-whets were heard when it was as low as -14 C. Boreal owls were heard most often when temperatures were between -10 and -5 C and saw-whets were heard calling most often at -5 to 0 C (table 4a). Temperatures rarely fell below -15 C in the lower elevations of the study area, so it could not be determined if extremely low temperature effected calling activity of saw-whet owls. The coldest temperature recorded during a census period was 25 C but there were high winds at the time and, although no owls were heard, this could have been due to the winds rather than the cold temperatures. Mikkola (1983) stated that cold temperatures, in combination with high winds, brought a pronounced reduction in calling of tawny owls (*Strix aluco*). Bondrup-Nielsen (1978) found that cold temperatures significantly reduced the calling rate of boreal owls but they were still heard calling in temperatures as low as -25 C. Mikkola (1973) found that most Tengmalm's owls were heard calling at temperatures between -10 and 0 C.

Precipitation

Snowfall (no rain was recorded during the study period), most of which was light, occurred at some time during 43% of the censuses that were conducted (table 4b). However, a majority of both species (75% boreal, 81% saw-whet) were heard calling when there was no snow falling. On only five occasions (2.8%) were boreal owls heard calling in heavy snow and saw-whets were never heard when there was heavy snowfall. Snowfall significantly reduced the activity of boreal owls (G test, $P < .05$) (Sokal and Rohlf 1969) whereas saw-whet owls were not significantly effected ($P > .05$) mainly because the lower elevations rarely received more than moderate snowfall (table 4b). Lundin (1961), Bondrup-Nielsen (1978), Holmberg (1979) and Korpimäki (1981) all found that boreal (Tengmalm's) owls call more frequently when there is no precipitation.

Table 4.--Frequency of boreal and saw-whet owls heard during different degrees of four environmental variables in 1984 in northern Colorado. G-test for goodness of fit was used to determine significant differences (Sokal and Rohlf 1969). BO-boreal, SW-saw-whet

4a	Temperature (% of occurrences)							
	<-20	-15	-10	-5	0	5	10	20
BO	0	5	15	34	32	9	5	0
SW	0	0	5	8	53	34	0	0

4b	Degree of precipitation % observed (%expected)				
	none	light	moderate	heavy	G-test
BO	75 (67)	16 (22)	7 (5)	3 (5)	$P < .05$
SW	81 (76)	16 (20)	3 (2)	0 (2)	$P > .05$

4c	% cloud cover -% observed (% expected)				
	0-25	26-50	51-75	76-100	G-test
BO	57 (56)	11 (9)	5 (6)	27 (30)	$P > .05$
SW	51 (56)	6 (5)	11 (14)	30 (27)	$P > .05$

4d	Approximate wind velocity (Beaufort scale)			
	0	1-2	3-4	>4
BO	65	21	12	2
SW	48	28	16	8

Cloud Cover

Cloud cover did not significantly influence either boreal or saw-whet owl calling activity (G test, $P > .05$), although both species were heard most often when there was a clear sky (table 4c). Lundin (1961) and Mikkola (1983) found that cloud cover only slightly affected Tengmalm's owl calling, whereas Bondrup-Nielsen (1978) found that it depressed boreal owl calling rates in one year but not another. Hansen (1952) found that tawny owls sang less on overcast nights and Mikkola (1983) found that eagle owls (*Bubo bubo*) called more frequently on calm cloudless nights.

Wind

Wind was the most difficult environmental factor to assess because it often obscured the

owls' calls. The boreal owl's primary call was difficult to distinguish in the wind while the saw-whet call is more distinct and could be heard more easily in windy conditions. On calm, clear nights both species could be heard from over 1 km but even moderate wind made hearing owls difficult from over 100 m. Of the 181 boreal owl contacts, 118 (65%) were when there was no wind, whereas over half (52%) of the saw-whet owls were heard in moderately windy conditions (table 4d). Lundin (1961) and Bondrup-Nielsen (1978) found that, of the parameters that they measured, wind had the greatest effect on boreal owl calling activity. Mikkola (1983) found that most (68%) Tengmalm's owls were heard in calm conditions and rarely were they heard in winds exceeding 30 km/hr.

Moonlight's influence on calling activity

Armstrong (1963) notes that some nocturnal singers are particularly stimulated by moonlight and Johnson et al. (1979) found that several species of owls, including saw-whets, were more vocal during a bright waxing moon. Contrary to this, Hansen (1952) reported that moonlight significantly reduced the calling activity of tawny owls. In this study, more individuals of both species were heard during the full moon than during any other phase (table 5), however, the difference was not statistically significant (G test $P > .05$). In the six years that censusing was done, 32% of all boreal and saw-whet owls were heard calling during a full moon, more than during any other phase. It is possible that, in years when calling activity is at a low level such as in 1981 and 1983, the owls may be stimulated by the moon but when calling activity is high, such as in 1984, the moon has less of an influence on calling. Lundin (1961) found that Tengmalm's owls often begin calling for the season during a full moon and continue calling regardless of the phase. In this study, a full moon appeared to stimulate the owls to begin calling for the the season in three of the five years that owls were heard.

OVERALL EFFECT OF ENVIRONMENTAL FACTORS ON SINGING ACTIVITY

The two factors that most affected calling activity of both species were wind and precipitation, and a combination of the two severely restricted calling activity. König (1968) and Mikkola (1983) suggested that approaching bad weather and low atmospheric pressure were likely to inhibit the calling of Tengmalm's owls. Generally, on my study area, bad weather was preceded by high winds which made censusing difficult and few owls were heard, but I do not know whether the wind or the approaching weather system negatively influenced the owls.

The conditions that were best suited for both listening effectiveness and calling activity of both species were a calm, clear night, -10 to 0 C, and a bright moon. Holmberg (1979 p. 243) stated that, "within certain limits, (calm, no precipitation, and temperatures not below -10 C) the weather seemed to exert little effect on the

Table 5.--The influence of the moon phase on calling activity of boreal and saw-whet owls in 1984. G-test was used to test for goodness of fit. (BO-boreal, SW-saw-whet)

	Moon phase - % of occurrences (% expected)					
	new	1/4	1/2	3/4	full	G
BO	16 (18)	24 (25)	16 (13)	20 (19)	28 (22)	>.05
SW	7 (9)	11 (16)	29 (24)	26 (26)	30 (25)	>.05

[Tengmalm's] owl's vocal activity." According to Korpimäki (1981 p. 17), the best time for hearing owls is on a "clear, quiet twilight night in late winter after a cold period." This is comparable to what I found in my study area.

MANAGEMENT APPLICATIONS

Over the six-year study period, the number of both boreal and saw-whet owls heard calling varied considerably from night to night and year to year, depending on several independent factors. True populations of both species probably stayed fairly uniform during this time but detectability was highly variable. The point transect method used in this study probably does not give accurate results for population studies, however it is valuable for determining the presence or absence of both species in the survey area. Although tape recordings were not used extensively in this study, they were found to be effective for locating saw-whet owls but not very effective for locating boreal owls.

For censuses to be used effectively, Holmberg (1979) recommended that they be conducted on at least three night in March (applied to most of Sweden). On my study area, the owls tended to call later in the year, and in order to detect owls, the censuses were most effective in April. Through most of the Rocky Mountain region in the United States, biweekly surveys conducted in March and April should be sufficient to detect populations of both boreal and saw-whet owls. A minimum of three years of censusing should be done in order to detect owl populations, as extremely low vocal activity in two consecutive years is fairly likely. To improve census efficiency, censuses should be conducted on clear, calm nights with moderate temperature (-10 to 0 C). Censuses should be timed so that at least one census is done during a full moon each month.

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Distribution and Status of the Boreal Owl in Colorado¹

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Abstract.--The Boreal Owl (*Aegolius funereus*) has been known in Colorado for over 90 years. Formerly listed as a rare winter visitor, the species has probably been a resident since the Pleistocene. Since 1979, intensive searches in northern Larimer County have documented four nestings. Apparently territorial Boreal Owls have been observed during the breeding season in 14 other counties. The species occurs mainly above 2900 m in climax spruce-fir (*Picea engelmannii*-*Abies lasiocarpa*) forests as far south as Wolf Creek Pass, 80 km north of the New Mexico border.

INTRODUCTION

The Boreal Owl (*Aegolius funereus*) has for years been considered a rare winter vagrant in Colorado (AOU 1957, Bailey and Niedrach 1965, Bent 1938, Karalus and Eckert 1974) and even some recent works do not show Colorado in the regular range of the bird (Alcorn 1986, Burton 1984, Godfrey 1986, Heintzelman 1984, Robbins *et al.* 1983). We therefore believe it useful to document the distribution and status of the species based upon records of specimens, photos, and field observations known as of 1986.

There is now considerable evidence that the Boreal Owl is a rather widespread species in sub-alpine forests throughout much of the state, with breeding season records as far south as Wolf Creek Pass (37°27'N, 106°52'W, elev. 3300 m), probably the southernmost known part of the species' range (cf. Voous 1960).

METHODS AND MATERIALS

Pertinent literature (both published and unpublished) was reviewed, primarily that in the Colorado State University Libraries, Fort Collins, and in the Denver Museum of Natural History. All known specimens (study skins, taxidermic mounts,

and skeletons) were examined to verify identifications and details regarding their collection. Records submitted to the Colorado Field Ornithologists were reviewed, as well as those received by Hugh Kingery, Regional Editor for *American Birds*. Notices concerning our interest in the dates and locations of sightings were distributed to Colorado Division of Wildlife and U. S. Forest Service field personnel as well as to active ornithologists. Intensive searches were conducted in the Cameron Pass area of Larimer and Jackson counties (Palmer and Ryder) and Spring Creek, Wolf Creek, and Slungullion Passes areas of Mineral and Hinsdale counties (Rawinski).

Locating Owls

Owls were located by listening for their vocalizations along roads and ski trails within the Cameron Pass area from January through June 1980-86. On calm nights Boreal Owls can be heard from over 1.5 km (Bondrup-Nielsen 1978). Each location at which an owl was heard was plotted on a USGS topographic map (1:24,000). If possible, the exact singing tree was located. Slight disturbances did not seem to deter the singing activity or cause the owls to move to other areas. In the 1983-84 surveys on Cameron Pass, no tape recordings were used to stimulate singing activity because this might have caused the owls to move, hence biasing the singing location. Tape recordings were used in 1980-82 and in 1985-86 to elicit responses and when trying to capture owls.

During road surveys, the observer stopped every 0.8 km along designated roadways and listened for 5 minutes before driving to the next stop (cf. Holmberg 1979). When a census was skilled or snowshoed there were no planned stops, but the observers listened for owls while moving, stopping occasionally to listen for distant owls.

The procedure used for locating Boreal Owls

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in the autumn was described by Palmer and Rawinski (1986).

Trapping Owls

Owls were trapped using mist nets and bal-chatri traps baited with a live mouse. Two 12 m by 2.6 m mist nets were set in a "V" formation and the bal-chatri trap, with the mouse, was placed at the closed end of the "V". Trapping began shortly after the owls began singing in the evening. Nets were placed in probable flight corridors within known Boreal Owl territories. A tape recording of the owl's primary song was broadcast from the area around the nets in order to attract the owl's attention. Captured owls were weighed, measured, banded, and equipped with a radiotransmitter.

Radiotelemetry

Male owls were equipped with transmitters using a criss-cross backpack attachment (Smith and Gilbert 1981) securing a 5-6 g single pulse transmitter with a 25 cm whip antenna. Because female owls frequently occupied a nest cavity, they were equipped with a 3-4 g transmitter attached to the central retrices using hot-melt glue (Bruggers et al. 1981) to avoid undue wear on the owl or the transmitter (Reynolds and Linkhart 1984). The larger transmitters had a range of approximately 3 km, ground to ground using a three element hand-held yagi antenna, while the 3-4 g transmitters had a range of about 1.5 to 2 km. Owls were recaptured to replace transmitters and to check on the owl's physical condition using either a telescoping pole with a mist net on the end (Reynolds and Linkhart 1984) or bal-chatri traps or mist nets placed by the roost site and baited with mice. Average life of the larger transmitters was 150 days, while the smaller ones had a life of about 60 days.

In 1983-84 in the Cameron Pass area attempts were made to locate the radio-equipped owls visually each day during the spring and summer and at least twice a week in the autumn and winter. At each roost the owls were observed for 0.5 to 2 h. Each roost location was plotted to the nearest 100 m on a USGS topographic map (1:24,000) using UTM (Universal Transverse Mercator) coordinates.

RESULTS

Specimens

Seventeen Boreal Owl specimens were located (9 study skins, 5 taxidermy mounts, and 3 skeletons). These specimens date back to 1896 (table 1). The first four were intentionally shot ("collected"), whereas all specimens preserved since 1970 were accidental deaths, primarily automobile roadkills. One (No. 14 in table 1) was caught in a kill-trap (Conibear) set for pine marten by another researcher. One specimen (No. 9) was originally misidentified as a Saw-whet Owl

Table 1.--Known specimens of Boreal Owls collected in Colorado.

Date	Where Collected	Specimen Located ¹	Sex	Age
1. 14 Oct. 1896	Crested Butte, Gunnison Co.	DMNH	♂?	?
2. Nov. 1903	Pitkin County	UNC	♀	?
3. 11 Nov. 1929	Fraser Grand Co.	DMNH	♂	?
4. 14 Aug. 1963	Deadman Mt., Larimer Co.	CSU	♀	juv.
5. 1 April 1970	Estes Park, Larimer Co.	DMNH	♂	adult
6. 15 June 1973	Rabbit Ears Pass, Routt Co.	CSU	♀	adult
7. 2 Feb. 1978	Evergreen, Jefferson Co.	DMNH	♂	adult
8. 6 Feb. 1978	Estes Park, Larimer Co.	CSU	♂?	adult
9. Feb. 1979	Rustic, Larimer Co.	FCM	♂?	adult
10. 14 July 1979	Trail Ridge Rd., Larimer Co.	DMNH	♂	adult
11. 7 Sept. 1979	Rabbit Ears Pass, Routt Co.	DMNH	♂	adult
12. 17 Dec. 1979	Estes Park, Larimer Co.	CDW	♀	adult
13. 19 Dec. 1980	Ranger Lakes, Jackson Co.	CSU	♀	adult
14. 12 Feb. 1984	Long Draw Rd. Larimer Co.	CDW	♀	adult
15. 7 July 1984	Chambers Lake, Larimer Co.	DMNH	?	nestl.
16. 7 July 1984	Chambers Lake, Larimer Co.	DMNH	?	nestl.
17. 7 July 1984	Chambers Lake, Larimer Co.	CSU	?	nestl.

¹Key: DMNH = Denver Museum of Natural History; UNC = University of Northern Colorado, Greeley; CSU = Colorado State University; FCM = Fort Collins City Museum; CDW = Colorado Division of Wildlife, Fort Collins.

(*Aegolius acadicus*) but was definitely a Boreal Owl. Unfortunately it was later stolen, but we have several photographs and measurements on file. Two of the skeletons are of nestlings found dead in an abandoned nest; a third nestling drowned in a small pond below the nest, apparently as it fledged. Specimens numbered 1-4 are cited in Bailey and Niedrach (1965). An alleged specimen reported to have been taken by Carter near Breckenridge on 28 December 1882 and reported by Cooke (1900) was later considered to have been an error either in identification or record-keeping (Lincoln 1929). Bailey and Niedrach (1965) thought Cooke had mistaken it for a Saw-whet Owl that Carter collected on that date.

Photographs

Not only have all known specimens been photographed, but numerous visual observations have been supported with 35 mm colored slides, a few of which have been published in black and white (Calder and Calder 1972, Kingery 1981, Palmer and Rawinski 1986). A minimum of 16 different Boreal Owls are believed to have been photographed (table 2). Some, such as the males which were radiomarked by Palmer near Cameron Pass, were photographed literally hundreds of times by many different photographers. Excellent photos of fledglings and an adult feeding young were taken by Art Wolfe 24-25 July 1982 at a nest along Corral Creek in Larimer County (Bergman 1985).

Table 2.--Boreal Owl records for Colorado, 1896-1986.

County	Specimens	Photos	Observations	Totals
Larimer	9	9	60	78
Hinsdale	-	3	6	9
Jackson	1	-	7	8
Grand	2	2	1	5
Summit	-	1	4	5
Gunnison	1	1	2	4
Mesa	-	-	3	3
Routt	2	-	-	2
Mineral	-	-	2	2
Boulder	-	-	2	2
Delta	-	-	2	2
Jefferson	1	-	1	2
Pitkin	1	-	-	1
Rio Grande	-	-	1 (?)	1
Gilpin	-	-	1	1
Totals	17	16	91	124

Observations

More than 90 observations of Boreal Owls are known for Colorado, most since 1963 and largely based on calls, many solicited by tape recordings (tables 2 and 3). These observations have ranged from north of Chambers Lake, Larimer County (40°31'N, 105°53'W) south to Wolf Creek Pass, Mineral County (37°27'N, 106°52'W) (fig. 1).

Owl Locations Based on Intensive Studies

A total of 36 Boreal Owls (9 in 1983, 27 in 1984) were located during an intensive study on Cameron Pass (Palmer 1986). Boreal Owls were found in areas with elevations ranging from 2770 to 3170 m (table 4). Seven Boreal Owl territories were used both in 1983 and 1984.

The highest density of Boreal Owls was found above 3000 m in mature spruce-fir forest interspersed with numerous subalpine meadows (table 5).

Trapping

Four Boreal Owls (2 males, 2 females) were trapped in 1983-84. One female was caught in a

Table 3.--Breeding season observations of Boreal Owls in Colorado.

Year	Minimum Number	Type of observation	Counties
1963	1	Specimen of juvenile	Larimer
1966	1	Heard	Larimer
1967	3	2 heard, 1 seen	Larimer, Summit
1970	2	1 specimen, 1 seen	Larimer, Gunnison
1971	1	Photo of juvenile	Gunnison
1973	1	Specimen	Routt
1974	1	Juvenile seen	Larimer
1975	1	Seen	Gunnison
1978	2	1 seen, 1 captured and released	Grand
1979	3	2 heard, 1 juvenile specimen	Larimer, Grand
1980	5	Heard	Larimer
1981	12	2 seen, 10 heard, 2 photos	Larimer, Grand
1982	15	5 seen, 5 photos, 5 heard	Larimer
1983	12	2 seen, 9 heard, 1 photo, 1 specimen	Larimer, Grand, Jackson
1984	27	8 seen, 21 heard, 7 photos	Larimer, Hinsdale, Jackson, Jefferson, Rio Grande
1985	13	Heard	Mesa, Boulder, Mineral
1986	1	Seen	Gilpin

Table 4.--Elevations of Boreal Owl territories, Larimer County, Colorado, 1983-84 (Palmer 1986).

Elevation (meters)	Number of territories 1983	1984
2701 - 2800	1	4
2801 - 2900	1	3
2901 - 3000	1	3
3001 - 3100	2	6
3101 - 3200	4	11
Total territories	9	27

Table 5.--Composition of habitat within Boreal Owl territories, Larimer County, Colorado, 1983-84 (Palmer 1986).

Habitat type	% of Habitat within territories (N=21)
Aspen (<i>Populus tremuloides</i>)	0.4
Lodgepole Pine (<i>Pinus contorta</i>)	8.9
Water	3.5
Road surface	1.5
Rocky terrain	0.5
Meadow	11.0
Spruce-fir	70.1
Timber harvest	0.8
Alpine tundra	3.4

mist net 22 September 1983 near Fraser by Tom Nicholls and radioed by Palmer and Ryder. The males were trapped on 17 May 1984, and a female was caught beneath a nest on 11 June 1984.

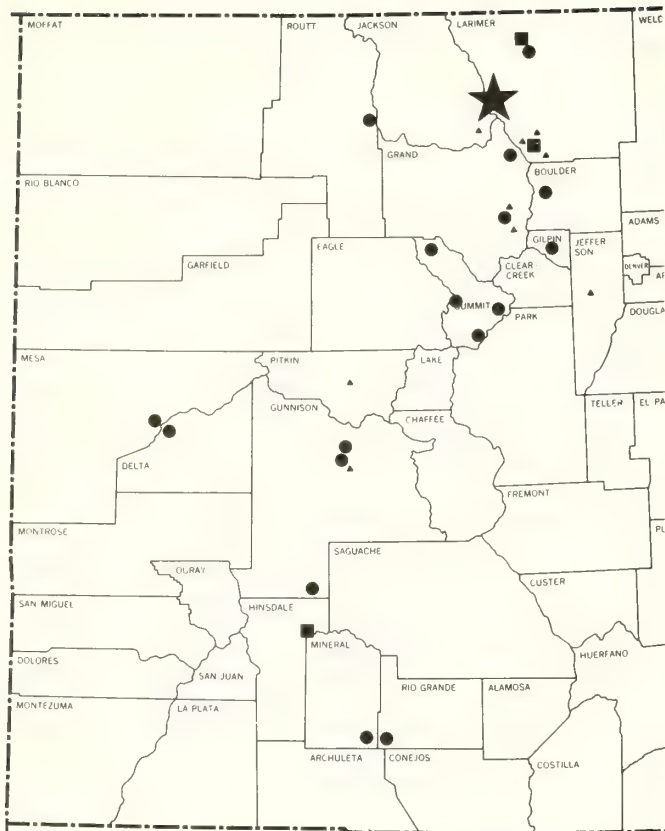


Figure 1.--Locations of Boreal Owl observations in Colorado. Breeding season records: ★ = >10; ■ = 6-10; ● = 1-5. Winter records: ▲ = 1-5.

Neither male was known to be nesting. Owls in 1984 were initially caught using a mist net baited with mice. Palmer found that playing tapes alone was not enough to attract the owls into the nets, but it did cause the owls to investigate the area and locate the mouse. The two males were recaptured a total of four times in order to replace the transmitters. Owls were recaptured for the first time using a telescoping pole with a mist net on the end, but when this method was tried on subsequent occasions the owls recognized it and avoided capture. A bal-chatri trap placed under a roost was successful once, and a mist net baited with live mice was used to recapture the owl on another occasion. Both of these methods were unsuccessful on subsequent capture attempts.

Roost Sites

One hundred seventy-four roosts (owls perched over one-half hour without moving) were located during the period (87 for radioed owl #1, 81 for #2 and 6 for #3) (table 6). Few data were obtained from the autumn-banded female. Only two roost trees were used more than once; one of these was used on consecutive days, while the other was used a week apart. All roosts were in coniferous trees. Engelmann spruce were chosen for roost trees significantly more (62.5%) than either subalpine fir (25.7%) or lodgepole pine (4.8%). No owls were found roosting in cavities.



Typical spruce-fir habitat in northern Colorado.

Feeding Ecology

Boreal Owls were observed hunting during the day on 27 occasions. Ten successful and three attempted kills were noted. On 10 other occasions, captive mice or birds were placed near an owl's roost in order to observe the owl's behavior, or in an attempt to recapture the owl. The general hunting techniques of Boreal Owls closely followed that described by Norberg (1970) except they often hunted during the day. Boreal Owls we observed often captured voles under moderate cover by plunging through the shrubs

Table 6.--Species of tree selected for roosts by Boreal Owls in north-central Colorado, 1984. Species of tree closest to the roost tree, a randomly selected tree, and the tree nearest to the random tree were used to test whether the owls preferred one species of tree in particular.

Tree Species	Roost tree	Nearest to roost	Random tree	Nearest to random
Engelmann spruce	116	67	76	79
Subalpine fir	48	96	79	78
Lodgepole pine	8	11	19	17
Total	174	174	174	174

Table 7.--Prey items taken by Boreal Owls in Larimer County, Colorado, 1981-84.

Prey species	Number and percent
Mammals	
<u>Clethrionomys gapperi</u>	39 (54.2)
<u>Peromyscus maniculatus</u>	1 (1.4)
<u>Microtus longicaudus</u>	9 (12.5)
<u>Microtus montanus</u>	9 (12.5)
<u>Sorex spp.</u>	4 (5.5)
<u>Eutamias minimus</u>	1 (1.4)
unknown	4 (5.5)
Birds	
<u>Turdus migratorius</u>	1 (1.4)
<u>Junco hyemalis</u>	2 (2.8)
<u>Parus gambeli</u>	1 (1.4)
unknown	1 (1.4)
Total	72

(Vaccinium spp. generally less than 10 cm tall) to get to the prey. Moving prey were captured more frequently than stationary prey, indicating that the owls may use auditory cues for locating prey even when the prey is clearly visible. No capture attempts were witnessed while there was snow on the ground, so it could not be determined whether the owls would penetrate beneath the snow to capture prey as reported by Nero (1980). Boreal Owls were seen with avian prey on three occasions, although the hunting technique used to capture them was not noted. Prey items as ascertained from observations, nest cavity contents, and analysis of regurgitated pellets are summarized in table 7.

Nesting

Four Boreal Owl nests were located during the period; one nest was used in consecutive years (Palmer and Ryder 1984). Two nests were in Engelmann spruce snags, and one was in a lodgepole pine snag. Nest heights were 6 m and 11 m in the spruce trees, 5 m in the lodgepole (table 8). Two Boreal Owl nests were in holes most likely excavated by Northern Flickers (Colaptes auratus) with entrance diameters of 80 and 78 mm, while the nest used in consecutive years was in a natural cavity with an entrance diameter of 100 mm. Probable nest initiation dates for the four nests were 17 April, 27 April, 10 May and 1 June.

Over 60 nest boxes, following Mebs (1966), were erected in the Cameron Pass area 1981-83. As of summer 1986, however, none had been used for nesting, although a few males were observed calling from near nest boxes.

DISCUSSION

After they collected a recently fledged Boreal Owl in north-central Colorado, Baldwin and Koplin (1966) theorized that the species "occurs in Colorado as a relict of a more widespread multilattitudinal Pleistocene population

Table 8.--Nestings of Boreal Owls in Colorado, 1981-84.

Year	Initiated	Nest Tree	Ht. of Cavity	Fate of Nest
1981	17 April	Lodgepole pine	5 m	4 eggs deserted
1982	1 June	Lodgepole pine	5 m	3 young fledged 1 egg dead
1984	27 April	Engelmann spruce	11 m	3 young, all died at fledging
1984	10 May	Engelmann spruce	6 m	1 egg deserted

of Boreal Owls." Such isolated breeding units in the Rocky Mountains would parallel a similar distribution throughout the species' Eurasian range (Mysterud 1970). The densities that we estimate from Colorado are comparable to densities of owls estimated by Bondrup-Nielsen (1978) in historic Boreal Owl range in Alberta and Ontario, Canada.

Boreal Owls have been seen or heard recently throughout the Rocky Mountain region: Colorado, Wyoming, Montana, Idaho and Washington (Palmer and Ryder 1984, O'Connell 1987). Nests have been documented in Idaho (Hayward and Garton 1983, Hayward et al. 1987). These records seem to indicate that a contiguous breeding range extends in the Rocky Mountains from Canada south to Colorado, supporting the theory advanced by Baldwin and Koplin (1966). The accumulation of records in recent years is more likely a result of greater human penetration into the Boreal Owl's habitat during the peak singing period rather than an increase in owl numbers in the region.

These findings, in conjunction with the discovery of Boreal Owls nesting in Minnesota (Eckert 1979, 1980), should justify a revision of descriptions and maps of the species' breeding range in North America.

POSTSCRIPT:

Rawinski and Stahlecker heard, recorded the voice, and photographed a male boreal owl 19 April 1987 along Dixie Creek in the Carson National Forest, New Mexico. At 36° 59' 28" North Latitude, this is, as far as we know, the most southerly record yet reported.

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Movements and Home Range Use by Boreal Owls in Central Idaho¹

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Abstract.--Radio-marked boreal owls moved an average minimum of 1265 m between consecutive day roosts. Winter roosts tended to be further apart than summer roosts. Boreal owls moved greater distances during years of lower prey densities. Males roosted an average distance of 2460 m from their nest. During a high prey year roost to nest distances were shorter than in subsequent years. Radio-marked owls used different home ranges during winter and summer. Summer activity centers shifted an average 2333 m from winter areas and increased in elevation by 230 m. The shift was probably due to the owls' need for cool summer roost sites and higher prey densities in high elevation spruce-fir forests. Year-round home ranges of 12 owls averaged 1528 ha (522-4119 ha), winter areas being larger than summer. Home ranges of adjacent owls overlapped extensively.

INTRODUCTION

Vertebrate movement patterns reveal resource requirements, degree of gene flow between geographic regions, level of population stability and the area necessary to support an individual in a particular environment. Information on movements and home range use by owls, however, is relatively difficult to gather due to their secretive behavior. Little is known about how these birds utilize space.

Although extensively studied in Europe, researchers have paid little attention to space use by the boreal, or Tengmalm's, owl. In North America, Bondrup-Nielsen (1978) followed two boreal owls in Canada and estimated their home ranges. Palmer (1986) intensively radiotracked two male boreal owls in Colorado in 1984 and reported movements and home range data. We are unaware of any other information on movements and use of space by this common forest owl.

Yearly movements by boreal owls have received greater attention than daily movements. Studies of yearly movements of boreal owls in the Old World (Lundberg 1979) indicate variation in site tenacity depending on environmental conditions and the sex of the individual. Site tenacity increases from northern to southern regions in Europe in response to snow cover and the amplitude and degree of synchrony of food fluctuations (Korpimäki 1986). In northern Sweden, male boreal owls are site tenacious between and during vole peaks while females are sedentary only during the vole peaks (Lofgren et al. 1986). Comparable information on site tenacity and nomadism is not available for North America, although Palmer's (1986) work also indicated a tendency toward a nomadic life strategy. Catling's (1972) information suggests the species is irruptive in eastern North America.

In this paper, we present preliminary information on the daily, seasonal, and yearly movement patterns in a recently discovered population of boreal owls in the mountains of central Idaho (Hayward and Garton 1983). Our paper is primarily descriptive. We do not intend to draw extensive ecological or life history conclusions from these data but rather present these preliminary results as an example of the movement patterns of a single population of boreal owls in North America.

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STUDY AREA

During the past three years we have studied habitat use by boreal owls (*Aegolius funereus*) in the mountains of central Idaho, USA. Our primary study area is Chamberlain Basin, located in the 850,000 ha Frank Church-River of No Return Wilderness. The basin, encompassing the headwaters of Chamberlain Creek, occupies about 25,000 ha of rolling mountain ridges rising from 1720 m to 2350 m elevation. The entire basin lies in the *Abies* life zone, and coniferous forest covers over 95 percent of the area. Lodgepole pine (*Pinus contorta*) dominates due to past fires (predominantly *Abies lasiocarpa* / *Calamagrostis rubescens* habitat type(h.t.)). Generally these stands are over 50 years old, some exceeding 120 years, and the forest structure is relatively open (tree spacing >2m). Large cavities are absent from these forests. At lower elevations, old-growth Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) stands occupy southern aspects (predominantly *Pseudotsuga menziesii* / *C. rubescens* - *Pinus ponderosa* h.t.) and mature to old-growth Douglas-fir (predominantly *A. lasiocarpa* / *Vaccinium globulare* h.t.) grow on more mesic sites which have escaped fire. Forest stands on these sites are multi-layered and often quite open. Cavities excavated primarily by pileated woodpeckers (*Dryocopus pileatus*) are abundant in stands where ponderosa pine snags are available. At higher elevations mature to old-growth subalpine fir (predominantly *A. lasiocarpa* / *V. globulare* and *A. lasiocarpa* / *V. scoparium* h.t.) dominates. Wet spruce bottoms (*A. lasiocarpa* / *Streptopus amplexifolius* h.t.), aspen stands (*Picea engelmannii* / *Equisetum arvense* h.t.), sagebrush-bunch grass slopes, and willow carrs occupy relatively small areas within the basin.

Travel within the study area is restricted to foot, skis, or horseback. An extensive trail system provides access to most of the basin, most areas being no more than 3 km from a trail. The wilderness character of the area provides an opportunity to study the habitat use and movements of the owls in an area free from road building, logging, and other human disturbances, or man-made habitats which might influence movements of the owls.

METHODS

Beginning in February 1984, we captured boreal owls using mist nests and bal-chatri traps. Trapping was restricted to within 4.5 km of our living quarters in the extreme eastern edge of the study area below 1800 m elevation. The owls were marked with 6 g backpack-mounted radio transmitters (Wildlife Materials Inc. model MPB-1220-LD) with an expected battery life of 150 days.

We monitored the movements of radio-marked owls from approximately January through August each

of 3 years (1984-1986), recapturing the owls to replace the transmitters periodically. During each field season, we worked at alternate study sites for two, 2-week periods. Therefore, radio-marked owls were not followed continuously.

Using hand held 3-element yagi antennas, the radio signal was audible from 0.5 to 11 km, depending on the topographic position of the owl and receiver. If an owl could not be located by checking from ridgetops within about 8 km of our station, we thoroughly searched the entire area within 14 km radius of the station (the entire upper basin) from fixed-wing aircraft.

We located radio-tagged owls on their daytime roosts and plotted the locations on 1:24,000 topographic maps. These locations were converted a cartesian coordinate system using the UTM system; locations were recorded accurate to 100 m.

In 1984, the marked owls were relocated on an irregular schedule ranging from 1-4 locations every ten days. In 1985 and 1986, we maintained a more regular schedule locating each owl every 2-3 days. Three times in 1986 we located an owl on its daytime roost on at least four consecutive days (different owls in each case). These locations provided some insight into day-to-day movements by the birds.

Each time we located an owl we spent one hour at the roost recording habitat information and observing the bird. On 17 occasions we watched birds on their daytime roosts for over two hours to document movements. In addition, on six days, an owl found actively hunting during daylight hours was followed to document foraging movements. On six nights we followed boreal owls during the first few hours of foraging activity. Night vision goggles used in conjunction with radio-telemetry aided in nocturnal observations. Three owls were marked with betalights (Hayward, in review) to further facilitate observation of the owls.

Analysis

In the analysis of distances between roost sites used on consecutive days or two days apart, the sampling units were mean distances for individual owls. The measurements of distances between roosts were considered subsamples and the mean distance between consecutive roosts (or roosts used two days apart in the second analysis) was calculated from these values. This procedure avoids problems of pseudoreplication; the distances between several roosts used by an individual owl can not be considered independent (Hurlbert 1984).

The analysis of roost to nest distances was limited to four male owls. The limited sample of owls constrained the analysis such that the sampling unit was each roost to nest distance.

Home range analysis was performed using the computer program HOME RANGE (Samuel et al. 1985) which computes home range estimates using three methods. Home range size was estimated using a

modification of Dixon and Chapman's (1980) harmonic mean measure of activity, Jennrich and Turner's (1969) bivariate normal ellipse, and the minimum convex polygon. Because the latter two estimates are not distribution free, as is the harmonic mean, we tested the distribution of owl relocations against the assumed distributions. If over half the owl home ranges differed from the assumed distribution for either the bivariate normal or minimum convex polygon we rejected those methods for a majority of the remaining analysis. Due to the prevalence of polygon home range estimates in the literature, however, we reported these estimates. In addition, our preliminary analysis of home range overlap calculates percent overlap using convex polygon estimates. We prefer to compare utilization distributions, but because our investigation is not complete, we have limited analysis to the current approach.

Prior to home range analysis we screened the input data for outliers, representing distant excursions from the normal activity areas. Extreme observations inevitably plague home range studies (Schoener 1981). Outliers in a bivariate test, defined as those points with bivariate normal weights lower than 0.6, were considered for removal. If the point represented a movement to an area over two km from the owl's normal use area and was used for less than three days, the point was removed.

Throughout the paper we have divided our field season into two periods, snow free and snow covered, which I will refer to as summer and winter. The period of snow cover each year was defined as the period from January (we entered the field in January each year) until over 50 percent bare ground was exposed on level ground at 1800 m.

All confidence intervals are calculated for $\alpha=0.05$, as are statistical tests. The information below summarizes the movement patterns of 12 boreal owls. Our sample of movements varied widely among owls (Table 1).

RESULTS

Daily Movements

We located consecutive daytime roost sites of 12 owls (4 females, 8 males) on 94 occasions. We feel these observations give an index of the minimum distance which the owl foraged during the previous night. Our evidence indicates that the daytime roost is likely near the end of the final foraging bout. Boreal owls observed foraging during daylight chose roosts within 50 m of their final foraging perch.

Distances between roosts on consecutive days ranged from 0 to 6816 m; mean distance being 1265 ± 374 m (Table 2). During winter consecutive roosts tended to be further apart than during summer. Mean distance, however, did not differ

Table 1. Monitoring period and number of relocations for radio-marked boreal owls at Chamberlain Basin. Only owls relocated on at least 10 occasions are included. The distribution of relocations for owls highlighted by * was significantly different from bivariate normal ($p > 0.10$) and those marked by t were significantly different from bivariate uniform ($p > 0.10$).

Boreal Owl	Sex	Monitoring Period	Number of Relocations	
			Winter	Summer
B033*	M	16 Mar - 22 Sep 1984	4	9
B034 ^t	F	31 Jan - 22 Sep 1984	10	9
B037**	F	5 Feb - 22 Sep 1984	16	8
B042	M	15 Feb - 22 Sep 1984	8	16
B043**	M	15 Feb - 5 Jul 1984	5	2
		17 Mar - 21 Aug 1985	19	14
		15 Jan - 29 Jan 1986	3	
B055 ^t	F	19 Mar - 7 Jul 1984	9	2
		23 May - 20 Oct 1986		41
B076**	M	18 Feb - 22 Aug 1985	24	19
B077*	M	18 Feb - 20 Aug 1985	31	14
B084*	M	31 Mar - 30 Aug 1985	12	17
		14 Jan - 29 Jan 1986	2	
B095 ^t	F	11 Mar - 7 May 1986	12	
B096**	M	26 Apr - 20 Oct 1986	5	53
B097**	M	25 Mar - 7 Jul 1986	13	27

significantly (winter: $n=11$ owls, $\bar{x}=1460 \pm 433$ m; summer: $n=7$ owls, $\bar{x}=868 \pm 483$ m). Three boreal owls in Colorado, averaged 708 m between consecutive day roosts (Palmer 1986).

Because we rarely located owls on consecutive days, we used distances between roosts located two days apart as a second index of the distance traveled by owls during their daily activities. This index provided a second sample with which to test differences in movement patterns between seasons and years.

Owls moved further between roosts in winter than summer but again, the differences were not significant (pooled data from the three years: winter $n=9$ owls, $\bar{x}=2204 \pm 1071$ m; summer $n=7$ owls, $\bar{x}=1069 \pm 427$ m). Considering winter and summer movements within any one year, differences were not significant. Point estimates of the mean, however, are all larger for winter than summer (Table 3). From 1984 through 1986, our indices of small mammal abundance declined (authors' unpublished data). Through this period of declining food supply, both winter and summer movements showed a trend toward longer movements between roosts (Tables 2 and 3). Although means are not significantly different, point estimates of the means consistently increased over the three years.

Another index of the minimum distance traveled by boreal owls during daily activity is provided by the distance between roost and nest sites of male owls during the nesting seasons. The mean distance between daytime roosts and the nest sites of four

Table 2. Ninety-five percent confidence intervals on the mean distances, in meters, between roosts used on consecutive days. Sample size in parentheses.

Year	Winter	Summer
1984	973±317(4)	502±5734(2)
1985	1638±897(4)	277±1993(2)
1986	1585±1399(4)	1157±1243(3)
Pooled (1984-1986):		
	1460±433(11)	869±483(7)

owls was 2460 m (±473m). Male owls rarely roosted within 500 m of the nest sites and on only one occasion ($n=43$) did a male boreal owl roost within 100 m of the nest site. Over 75 percent of roosts were located over 1000 m from the nest and up to 5600 m from it. The distance between roosts and nest sites showed no significant tendency to increase or decrease during the course of nesting (incubation through fledging). In 1984, when our index of prey availability was higher than the following years, roost to nest distances were significantly less than those measured for an owl in 1986 (Table 4).

Although radio-telemetry (triangulation) indicated male owls did some foraging near the nest site, we feel the birds frequently foraged at the distances indicated by the roost to nest distances. Following prey deliveries at the nest on three nights, one owl returned to the area of its daytime roost several km from the nest. During the incubation period, male owls generally visited the

Table 3. Ninety-five percent confidence intervals on the mean distance, in meters, between roosts located over a three-day period (one day separating each roost location). Subsamples are unequal among owls and reported sample sizes indicate the number of owls. Data include 130 distances.

Year	Winter	Summer
1984	1335±1390(3)	
1985	1753±430(5)	802±1192(3)
1986	4551±10,323(2)	1380±751(3)
Pooled (1984-1986):		
	2205±1071(9)	1069±427(7)

Table 4. Distance in meters between daytime roosts and an owl's nest site for male boreal owls during incubation and nestling periods.

Year	Owl	n	Mean ± 95% Bound	Range
1984	B033	6	1676(±383)	1334-2062
	B042	9	1333(±865)	100-3220
1985	B077	3	4096(±2825)	2802-5166
1986	B097	25	2886(±667)	583-5608

nest 1-3 times each night. Later in the breeding season the male may visit the nest as many as 10 times in a night.

Foraging

Observation of hunting owls on ten occasions, totaling 18.6 hrs, provided some indication of travel rate, distances between hunting perches, and duration of perches--measures of hunting behavior. During these observations, the owl was not always visible, so some hunting perches used very briefly were overlooked.

We measured the total distance covered by the foraging owl during the observation session by plotting its path on 1:24,000 topographic maps. Although these measurements are not particularly precise, they can be used to calculate a minimum travel rate while foraging (by dividing by the observation period). Foraging owls traveled from 1 to 36 m per minute with a median rate of 10 m/min for the 10 observation sessions. The owls remained on each hunting perch from a matter of seconds to over 1/2 hr ($n=94$, $\bar{x}=6.35\pm1.6$ min). Prior to locating prey, the owls tended to move more rapidly, remaining on each perch 2-4 minutes. After detecting prey, however, an owl often remained on a perch for over 10 minutes before pouncing on the prey.

The distance traveled between perches was not always estimated, but for sixty estimated distances, the mean flight distance was 33 m (±8.3 m). This estimate is negatively biased as flights longer than 50 m often could not be estimated because the owl moved again before the perch was located.

While foraging, the owls concentrated their activity in a relatively small area compared to the total length of the foraging flights. The owls we followed doubled back frequently, and thus covered a relatively small rectangular area rather than a long narrow path.

Diurnal Movements

Owls were generally sedentary during daylight, rarely moving more than 50 m. Frequently, however, the roosting birds became active during mid-day and moved 5-20 m to a new roost or to cached prey. In 1986, movements from roosts were often associated with retrieval of cached prey, avoidance of sun, or disturbance due to high winds. On 17 occasions when roosting owls were observed more than two hours, the owl changed roosts 71 percent of the days. The new roost was an average of 27 m from the first roost. Palmer (1986) noted roost changes during 56 percent of observations.

Although not quantified, we noted an increase in diurnal foraging over the three year period. In 1984, we rarely observed our radio-marked owls foraging during daylight. In 1985, four marked owls occasionally hunted during the day. During the autumn of 1986, however, we observed two marked owls hunting nearly one third of the days radio-tracked. This frequency was higher than at any other observed period. Palmer (1986) observed hunting on 15 percent of summer locations.

Seasonal Movements

Radio-marked owls consistently used different home ranges during winter and summer. Harmonic mean center of activity (defined by the minimum harmonic value in an analysis of roost locations (Samuel et al. 1985)), shifted a mean of 2333 m (± 1518) between winter and summer for seven owls (limited to birds with 8 or more locations each season). Six of these owls used summer home ranges to the west of winter areas. The smallest shift between winter and summer activity centers was made by the only owl whose activity center moved eastward. Our study area generally rises in elevation from east to west indicating that roost locations shifted to higher elevations in summer. In fact, the elevation of winter ($n=10$, $\bar{x}=1807\pm 71$ m) and summer ($n=11$, $\bar{x}=2038\pm 121$ m) activity centers was significantly different. Considering only owls with over eight observations in each season, the difference in elevation was also significant ($p=0.008$, Wilcoxon matched pairs sign rank).

Nest sites of radio marked owls (5 nests), were all located in the lower 1/3 of the study area. During the winter prior to nesting, the home range activity center for five marked owls (3 females, 2 males) could not be shown to differ from the nest location (mean distance of activity center to nest, 1364 ± 1927 m; not significantly different from zero). Summer home ranges defined by roost locations, however, were not centered on nest sites but averaged 2126 m (± 1967 m) away (2 females, 5 males). Nest sites were generally on the periphery of summer home ranges.

During nesting, female activity was restricted to the immediate vicinity of the nest. During incubation the female left the cavity once or twice during the night for about 15 minutes, flying 30-60 m (observations at three nest sites and camera records at another). After the eggs hatched, she

left more frequently but only for brief periods (10-20 min) and one female was observed (through night vision goggles) carrying debris from the nest.

Female behavior following the brooding period (generally to nestling age of 20-25 days) was variable. Considering radio-marked females at four nests which produced fledglings, on only one occasion did a female consistently participate in feeding the young. One female moved out of the study area when she left the nest (young 21 and 23 days old) and another female who nested in 1984 and 1986 was only known to have delivered prey to the young on two nights in 1986 after leaving the nest three days earlier. She remained in the basin following nesting but concentrated activity about 5 km from the nest. In this case the male owl had abandoned the nest six days before she left and the young ultimately perished.

Home Range

In this section, we would like to summarize preliminary information related to how the owls utilize space. How did the owls distribute their use of space throughout their home range? What differences, if any, exist in utilization distributions between winter and summer? How large are intensively used areas (i.e. core areas)? And how broadly do seasonal home ranges overlap among owls? These results, however, must be considered preliminary as we have not completed fieldwork and, due to time constraints, the analysis has not included some sophisticated techniques for dissecting the internal anatomy of home range (Samuel and Garton 1985).

Here we define the home range as that area traversed by the individual in its normal activities of food gathering, mating and caring for young (Burt 1943). The utilization distribution (UD) describes the proportion of total activity that takes place in a given area. The UD, then, is useful in describing how an individual uses space within its home range in relation to environmental features. Core areas are those portions of the utilization area used more frequently than others.

We analyzed the home ranges of twelve radio-tagged owls monitored for various periods from 1984-1986. We compared the distribution of relocations for seasonal and overall home ranges to a bivariate normal and bivariate uniform distribution to test the underlying distributions required for the Jennrich and Turner (1969) and minimum convex polygon methods (Samuel and Garton 1985). Samuel and Garton (1985) suggested a minimum of 30 relocations and $\alpha=0.10$ for sufficient power to test the assumed distributions. Considering seasonal and overall samples with over 30 relocations, we rejected the assumption of bivariate uniformity in 8 of 10 cases and rejected the assumption of bivariate normality in 9 of 10 cases. Due to this high rejection rate we preferred a distribution free analysis utilizing the modified harmonic mean UD (Dixon and Chapman 1980) in the program HOME RANGE (Samuel et al. 1985).

Home ranges of boreal owls in Chamberlain Basin were quite large. Considering our locations of twelve owls (each with 10 or more relocations) 85 percent UD's covered an average of 1528 ha (± 687) (Table 5). The large overall utilization distributions (range of 85 percent contours 522-4119 ha) reflect the shift in areas used in winter and summer.

Mean seasonal home ranges were substantially smaller than the respective overall home range (Tables 5,6). This difference could be due to a smaller sample of locations for seasonal home ranges or simply show that smaller areas are used in any one season than the year round home range. Our simulations (unpublished data) indicate that harmonic mean measures of home range are slightly influenced by sample size but not to the extent seen in Tables 5 and 6. Furthermore, correlations between sample size and home range size from the owl data were low. In seven of nine tests, correlations were below 0.3. We conclude that the area required to support an owl during a given season appears to be less than the area required to meet the birds' needs for an entire year. No difference can be shown for mean area of UD's between seasons (t-test, Table 6). A Wilcoxon matched pairs, sign rank test ($n=5, p=0.125$), considering only owls with at least eight locations for each season, also showed no seasonal differences.

Table 5. Home range size of boreal owls at Chamberlain Basin. Percent utilization distributions (UD's) were calculated using the program HOMERANGE (Samuel et al 1985). Minimum convex polygon estimates are reported only for comparison with literature as few distributions corresponded to the assumed bivariate uniform for this estimate.

Year	Owl	n	Area of UD (ha)			Minimum Convex Polygon (ha)
			35%	55%	85%	
1984	B033	13	158	311	639	557
	B034	19	72	168	522	627
	B037	24	335	931	2723	2688
	B042	24	102	343	602	776
1985	B043	35	332	812	1813	2789
	B076	43	269	623	1992	1052
	B077	46	308	922	1937	1736
	B084	29	291	681	1490	1555
1986	B055	40	83	445	886	2293
	B095	12	77	278	534	3496
	B096	57	187	478	1076	1098
	B097	40	709	1357	4119	2507
Mean \pm 95% Bound			244 \pm 114	612 \pm 220	1528 \pm 687	

Table 6. Seasonal home range size (ha) of boreal owls in Chamberlain Basin with 10 or more relocations. See text and Table 5 for details on calculating the estimates.

Season	Year	Owl	n	Area of Utilization Distribution		
				35%	55%	85%
Winter	1984	B034	10	26	113	311
		B037	16	87	303	970
	1985	B043	19	159	429	1170
		B076	24	121	313	1057
		B077	31	283	669	1714
		B084	12	152	357	807
	1986	B095	12	77	277	534
		B097	13	121	351	1962
		Mean \pm 95% Bound			128 \pm 62	352 \pm 130
	Summer	1984	B042	16	113	168
1985		B043	14	2	197	446
		B076	19	8	56	158
		B077	14	124	427	924
		B084	17	63	335	1030
1986		B096	53	148	361	820
		B097	27	236	739	1837
		B055	40	190	423	1023
Mean \pm 95% Bound			111 \pm 69	338 \pm 173	845 \pm 421	

The owls concentrated their activity in a small portion of their seasonal home ranges. In general, this is demonstrated by comparing the areas encompassed by the average 55 percent and 95 percent harmonic contours for winter and summer which indicates the owls concentrated over half of their activity in one quarter of the home range. In winter the mean 55 percent harmonic contour for 8 owls encompassed 24 percent of the area circumscribed by the mean 95 percent contour. Likewise, the ratio for summer was 30 percent of the area. During any one season, most owls concentrated their activity in two or three areas within the home range and explored other areas infrequently. The owls rarely stayed in a particular area for more than two to three weeks; rather, they moved among two or three core areas. Relocations of two owls demonstrate the pattern of use confined to particular core areas (Figs. 1,2). The summer home range of a male boreal owl (B096) shows three areas of relatively high use separated by unused forest (Fig. 1). The winter home range of another male (B077) exhibits this same pattern of non-uniform use of space (Fig. 2).

Home Range Overlap

Seasonal home ranges of radio-marked owls overlapped extensively each year of the study. Because of the low number of relocations for each owl in 1984, we restricted analysis of overlap to the last two years. In the winter 1985, the home range of B077 (estimated by minimum convex polygon) encompassed 82 percent of the area used by B084. The complementary overlap (B084-B077) was 43 percent (Fig. 3). Measurements and behavior indicated both owls were males. During summer 1985 these same owls overlapped 51 percent (B084-B077) and 80 percent (B077-B084). In the summer and autumn 1986, three adjacent owls, including a mated pair and another male from a failed nest used much

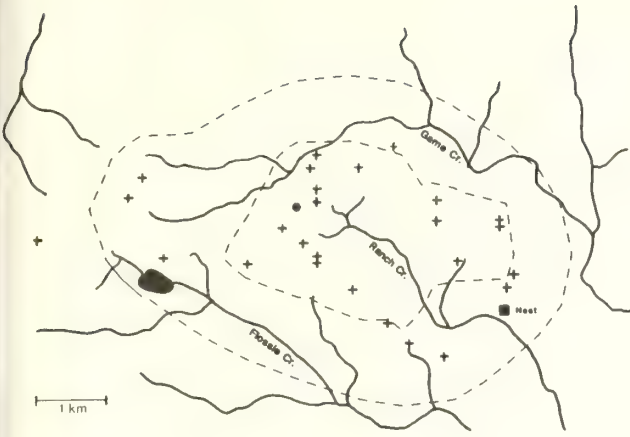


Figure 1.--Summer home range of a nesting male boreal owl. Concentric lines represent 95 percent and 55 percent utilization distribution contours. A "+" indicates individual locations; "*" represents the activity center.

of the same area (Fig. 4). Overlap values among these three owls ranged from 21 to 80 percent and averaged 51 percent. The two males' home (BO96, BO97) ranges overlapped 39 and 63 percent.

The degree of overlap in use of space among unmated boreal owls was further demonstrated in daily radiotracking records. On 1 May 1986 two males, each known to be singing nightly at nest sites separated by 2.4 km were found roosting within 200 m of one another. On the night of 14 February 1984, three boreals, two known to be males, were caught in the same mist net. Likewise,

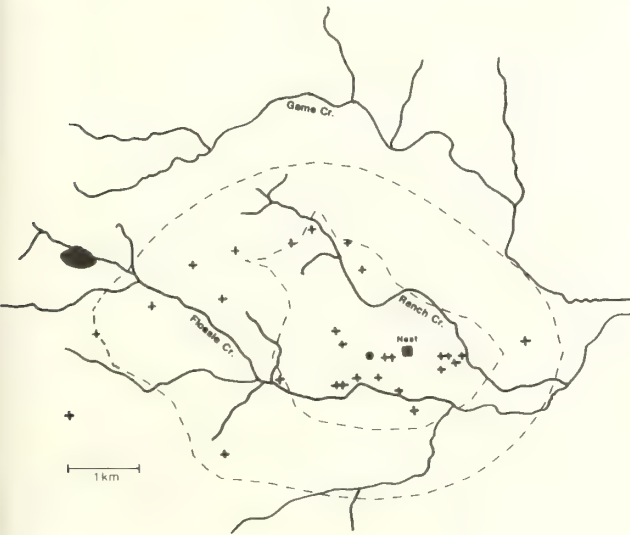


Figure 2.--Winter home range of a male boreal owl who nested the following May. See Figure 1 for details.

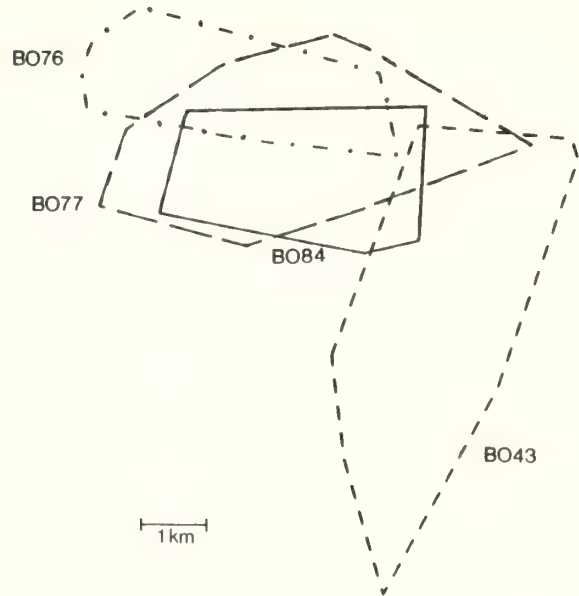


Figure 3.--Home range overlap among four male boreal owls during the winter 1985.

on 18 February 1985, two males were caught in a mist net. Two owls which ultimately mated were located roosting within 10 m of one another on 23 March 1984, 0.9 km from the nest of that year. On five other occasions prior to nesting, however, the members of the pair were never less than 1 km apart.

Year to Year Movements

Movements of radio-marked owls provide some indication of the degree of site tenacity in the Chamberlain Basin population. Four owls, one

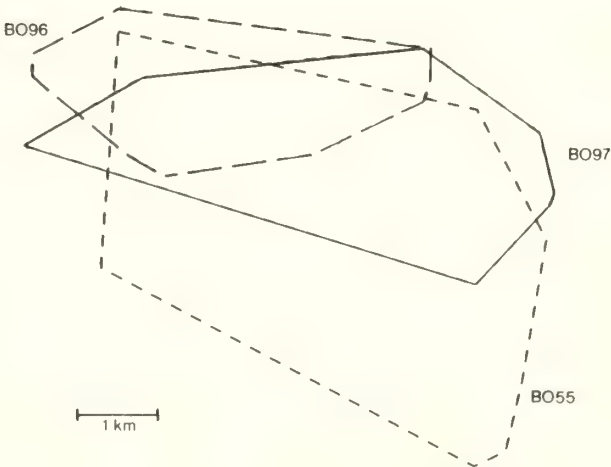


Figure 4.--Home range overlap among three boreal owls during summer 1986. Boreals 97 and 98 were a mated pair, 97 being the male. Boreal 96, a male, attracted a mate who abandoned prior to laying.

female and three males, were found in the Basin in more than one year. The female nested with a different mate in 1984 and 1986 in cavities 1.4 km apart. A male captured 14 February 1984 was recaptured 17 March 1985, 0.5 km away from his first capture site. This owl (B043) wore an active transmitter from March 1985 through January 1986 when it moved out of the basin with a fresh (11 day old) transmitter. A second male (B085), captured at its nest in 1985, was using a home range within several km of the nest February 1986 when it died (cause thought to be starvation). The third male, first captured in March 1985 (B084) was using a similar home range in February 1986 when it left the basin (same two week period as B085 died and B043 left). This owl's radio signal was relocated on 7 May 1986 80 km to the west near Upper Payette Lake, Valley Co., Idaho.

One female was thought to have left the basin within 8 days after she first left her nest. On 5 July, when her young were 20 and 22 days old, the owl was roosting near the cavity at 2100 h, the first day she was found off the nest. By 2207 h she was moving from the nest and could not be located until 13 July when a faint signal was heard about 7 km from the nest. The radio signal was never heard again.

A male also appeared to have left the Basin when he abandoned his nest 17 days into the nestling period. A camera at the nest failed to register any nest visits the night after we first failed to locate his radio signal. Whether the owl was killed by a predator, which also destroyed the radio, or the bird left the region is unknown.

DISCUSSION

Our results reveal six important features about boreal owls at Chamberlain.

- 1) Boreals used large seasonal areas for birds of their size.
- 2) Differences in seasonal home range and movements indicate that resource requirements likely differ substantially between seasons, and at Chamberlain all those requirements are not met within one forest type.
- 3) Use of space within seasonal home ranges was not uniform but concentrated in particular core areas.
- 4) The owls did not maintain exclusive territories but overlapped broadly in seasonal home ranges.
- 5) During the period of declining prey resources (1984-1986), the distances moved between roosts tended to increase.
- 6) The pattern of year to year occupancy indicated a mixture of nomadic and sedentary behavior.

Boreal owls used extremely large areas at Chamberlain. Despite our relatively small sample of relocations, estimated home ranges were larger

than the 1-5 km² reported by Bondrup-Nielsen (1978) for boreal owls in Canada. Home range sizes for three males in Norway ranged between 94 and 226 ha (Jacobsen and Sonnerud, these proceedings). Breeding season minimum convex polygon home range estimates for two Colorado male boreal owls (240 and 352 ha, minimum convex polygon) (Palmer 1986) were similar to summer home ranges calculated for two males nesting in our study area the same year (317 and 335 ha).

Home ranges reported for other species are also substantially smaller than Chamberlain boreal owls. Forsman et al. (1984) cited home ranges less than 2000 ha for spotted owls (*Strix occidentalis*), while Forbs and Warner (1974) reported 113 ha home ranges for Michigan saw-whet owls (*Aegolius acadicus*). Smith and Gilbert (1984) calculated 103 and 130 ha home ranges for Connecticut screech owls (*Otus asio*) radiotracked for five months (January - May). Boreal owl home ranges fell within the range reported for the large eagle owl (*Bubo bubo*) of Europe (1400-15,000 ha) (Mikkola 1983). The use of such a large area by a relatively small owl indicates either low resource abundance or that areas of resource concentration are widely dispersed.

In the heterogeneous habitat at Chamberlain, all resource requirements were not met by contiguous forest stands. Thus, seasonal requirements were satisfied in different areas. This feature is reflected in changes in location of home ranges from winter to summer accomplished by a shift to higher elevations in summer, and by the consistent trend for winter movements to be longer than summer. Also, the nest site was never centered in home ranges, rather, roosting and foraging habitat was chosen distant from the nest site. In Colorado, the home ranges of boreal owls shifted after the breeding season (Palmer 1986). Such a shift might also indicate changing resource needs and availability.

In winter, movements are likely primarily directed toward securing sufficient prey to meet daily maintenance costs. Specific areas may be used because they provide higher than average prey availability or lower the owls' average energy costs. Our observations indicate that daytime roost requirements play little role in dictating winter movements and home range. In summer, however, roost site requirements may be partly responsible for the shift to high elevations away from the nest site. Boreal owls are easily heat stressed; guller fluttering by inactive roosting owls occurred at temperatures as low as 75°F. Prey availability might also play a role in choice of space during summer since the same cool, mature forests which provide optimum summer roosts also have the most abundant small mammal populations (unpublished data). Areas of abundant cavities were distant from the high elevation forests so that nest sites were usually distant from roosting and foraging areas.

The concentration of activity in small portions of seasonal home ranges in Chamberlain and

suggestion that forest stands varied in their value to boreal owls. Future analysis comparing the habitat within core areas to less used portions of the home range may indicate what features of forest structures and composition are important in boreal owl habitat.

Territories of boreal owls in Europe (Solheim 1983) and Canada (Bondrup-Nielsen 1978) have been characterized as simple breeding territories with no defense of foraging areas. Only a small region around the nest is defended as an exclusive area. Our information shows that boreal owl movements are not influenced by conspecifics and overlap among owls is substantial. In Norway, male boreal owls averaged 56% overlap (Jacobsen and Sonerud, these proceedings). Palmer (1986) also found two male boreal owls overlapping as much as 98 percent in early summer. Defense of the large foraging areas used by the owls would be difficult if not impossible.

From 1984-1986, during a period of declining small mammal abundance, home range size tended to increase as well as the length of day to day movements. Faced with lower prey availability, two basic strategies may be employed. First, the owls may conserve energy through reduced foraging activity and/or reproductive expenditure. An alternative strategy is to increase foraging effort at the expense of other activities. Increased activity may make the owls more vulnerable to predation. During winter, a majority of the energy expenditure is for self maintenance. Because boreal owls are relatively small birds, they cannot rely on accumulated reserves for extended periods. A strategy of energy conservation, therefore, is not feasible. Instead, the owls appeared to search over progressively larger areas as prey resources declined.

During summer, energy expenditure may be directed toward reproduction as well as self maintenance. The range of strategies to cope with reduced prey is, therefore, increased. Breeding efforts may range from failure to initiate nesting through raising a large brood, with corresponding variation in energy expenditure. At Chamberlain, the number of calling owls decreased and frequency of nest abandonment increased as prey resources declined indicating a reduction in reproductive expenditure. In addition, summer home ranges and daily movements increased from 1984-1986.

Populations of boreal owls vary in the degree of site tenacity or nomadism which they exhibit. In Europe, there is a general trend for increased nomadism in more northern populations (Korpimäki 1986). Korpimäki (1986) found that within Finland the degree of nomadism was positively correlated with winter snow depth. Lundberg (1979) hypothesized that due to the conflicting pressures of food stress favoring nomadism and nest site scarcity favoring site tenacity, the movement pattern of male and female boreal owls differ. He hypothesized that males would exhibit site tenacity and females nomadism. Lundberg's reasoning finds support from theory and empirical evidence. The

large potential clutch size of boreal owls and cyclic pattern of food production fit Andersson's (1980) model for a species likely to exhibit nomadism. On the other hand, von Haartman (1968) showed that residency was favored by the increased reproductive output afforded by early nesting in cavity nesters. Wallin and Andersson (1981), Solheim (1983), Lofgren et al. (1986) and Korpimäki (1986) have demonstrated that boreal owls exhibit both site tenacity and nomadic tendencies. In the most intensive investigation, Lofgren et al. (1986) showed that males were site tenacious throughout a prey cycle whereas females were tenacious only during prey peaks.

Our owls also showed a mixed strategy of site tenacity and nomadism, but differences between sexes were not clear. Some males and females remained in the study area during a period of declining prey. Both sexes also exhibited nomadism during the same period. The only individual located far from the study area was a male, but several others disappeared from the area and were never relocated. In Colorado, Palmer (1986) also observed a tendency toward nomadism in both male and female owls.

Deep snow (0.5-2.0 m) which remains in our study area for five months each year and relatively low prey populations likely contribute to the nomadic character of the boreal owl population at Chamberlain. Winter prey scarcity may frequently force many owls to search elsewhere for food. Conversely, if prey populations fluctuate but do not exhibit a cyclic pattern, the tendency for nomadism should be reduced (Andersson 1980). Small mammals in the Rockies have not been shown to be cyclic. The conflicting forces of severe winter food scarcity but lack of a consistent cycle may be responsible for the mixed pattern of site tenacity and nomadism.

SUMMARY

The boreal owls we studied moved over large home ranges throughout the year. Within seasonal home ranges, the owls concentrated their activity in several core areas, frequently moving back and forth among preferred areas. The owls consistently shifted seasonal ranges, concentrating activity at higher elevations during summer months. Despite this shift to higher elevations during breeding, nest sites were all within the lower one third of the study area and were generally on the periphery of the home range. Although not conclusive, our data suggested that the owls used larger home ranges and moved further from one day to the next during a period of declining prey.

As indicated by other authors, we found no evidence of defense of foraging areas. Home ranges of owls overlapped extensively and male boreal owls were found roosting within 200 m of one another. A mixed pattern of sedentary and nomadic behavior was indicated by year to year movements.

ACKNOWLEDGEMENTS

L. Flaccus and A. Wright helped radiotrack owls. The U.S. Forest Service, Forest and Range Sciences Laboratory, Boise, Idaho, and Idaho Department of Fish and Game provided major funding. The N.A. Bluebird Society, U.S. Army, Max McGraw Wildlife Foundation, U.S. Forest Service Region I, Columbia Basin Audubon Society, TDK Electronics Corp., and Duracell Corp. also gave support. Payette National Forest provided housing. The study could not have been completed without the support of all the above individuals and organizations.

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Occurrence of the Boreal Owl in Northeastern Washington¹

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Abstract. Until its first documented nesting south of Canada in Minnesota in 1978, the Boreal owl was considered to occur only as an accidental in the United States. Since that time, the species has been found elsewhere in the United States (Colorado and Idaho). With the knowledge of the bird's habitat preference, a search was made for the location of habitat and then the birds. Maps showing all Engelmann spruce (*Picea engelmanni*), Subalpine fir (*Abies lasiocarpa*) timber types were used to define potential Boreal owl habitat. During parts of 1985 and 1986, Boreal owls were found during all seasons of the year. Although a nest was not located, one juvenile bird was found.

INTRODUCTION

Heretofore only three documented sightings of Boreal owl (*Aegolius funereus*) existed for the state of Washington. The first bird was collected in January 1905 in Whatcom County, Western Washington, but as Johnson & Hudson (1976, Auk 93: 195-196) pointed out it unfortunately soon disappeared resulting in questionable identity. A second specimen was obtained on January 10, 1974 in Pullman, Whitman County, Eastern Washington by Richard E. Johnson (Batey, et al, 1980). In May and June of 1979 a pair and eventually two or three fledglings were observed in a back yard in Pullman, Washington (Batey, et al, 1980).

Although fledged Boreal Owl juveniles were seen in Colorado in 1963 (Baldwin & Koplin, 1966) and in Montana in 1973 (Skaar, 1975), it wasn't until 1978 that the first documented nesting of the Boreal Owl occurred south of Canada; in Cook County, Minnesota (Eckert & Savaloya, 1979). This did not extend the established breeding range (A.O.U. 1957), because the observation was made so close to the Canadian border. However, two subsequent nesting records did extend that range. Hayward & Garton's (1983) observations demonstrated that a resident population is established in the mountains of Central Idaho. They concluded that the presence of this resident population of Boreal Owls supported Baldwin & Koplin's (1966) hypothesis that the breeding range of this species extends southward along the Continental Divide. To further substantiate

this hypothesis, Palmer & Ryder (1984), found nesting Boreal Owls observed or heard throughout the Rocky Mountain Region (Colorado, Wyoming, Montana, Idaho and Washington). Knowing this and the fact that the Kettle River Range and the Selkirk Mountains of northeastern Washington are "foothills" of the Rocky Mountains and a part of the Rocky Mountain Region, my associate Bart Whelton and I thought it possible that the Boreal Owl might be found here as a permanent resident.

STUDY AREA

The Selkirk Mountains of northeastern Washington are characterized by many peaks over 1500 meters in elevation with some exceeding 2100 meters. Much of the area over 1500 meters



Figure 1.--Spruce-fir forest along the Colville-Kaniksu divide.

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is covered with a forest of climax spruce-fir (*Picea engelmanni*-*Abies lasiocarpa*) similar to that found in the areas searched by Palmer & Ryder. This spruce-fir forest is a boreal forest type very similar to that of northwestern Canada with the major difference being that the Engelmann spruce is replaced by Black Spruce (*Picea mariana*) and White Spruce (*Picea glauca*). The spruce-fir stands usually have a crown closure of less than 70% interspersed with small



Figure 2.--Boreal Owl habitat in the Selkirk Mountains of the Colville National Forest.

openings and larger mountain meadows. This is the forest type which Boreal Owls apparently prefer (Palmer & Ryder, 1984).

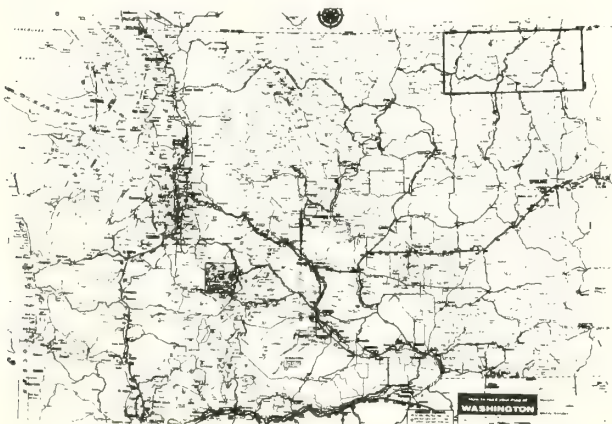


Figure 3.--Map of Washington state with the study area outlined.

In northeastern Washington both the Kettle River range and the Selkirk Mountains are located within the confines of the Colville National Forest. I visited the Forest Supervisors office where I studied their timber type maps and transferred the Engelmann spruce and Alpine Fir types onto a copy of the Colville National Forest map. A timber type is one named for its major volume species regardless of tree size, however, it may and in these types most often does, contain other species. Our field investigations began in late April of 1985 and continued periodically throughout 1985. Since this effort was a spare-time project, it was conducted whenever possible usually on weekends. A tape of the winnowing call (Bondrup-Nielson, 1984) was played in or near the appropriate habitat, usually at one quarter mile intervals, during the nighttime hours. The first response was obtained in Sherman Pass on the night of April 27 from a male giving the winnowing call. When we continued playing the call the bird approached and lit on a nearby tree. Each of the responses obtained at later dates were defensive in nature; either the SKIEW call or the OO-WORK call. When emitting these defensive responses the birds were very close to us (30-35 meters) and at times flew directly in our faces or over our heads. Whether they came some distance before giving the call or we just did not hear them until they were close by, we are not sure. It is my opinion that they were on territory when we approached them with the call and consequently they responded from wherever they were upon hearing our recording. A very small part of the existing habitat was searched because of difficult access and limited time.

Nevertheless, of 5 different sites composed of the spruce-fir habitat that were visited on one or more occasions between April 27 and December 15, 1985, Boreal Owls were found at each site on at least one occasion. At one site (Salmo Pass) the birds were located in the same locality in three different months (June, July and September). In all but one instance the birds were found at over 1580 meters elevation. The owls that were found below 1580 meters were located in December and were occupying a forest composed largely of lodgepole pine (*Pinus contorta*) with a mixture of the typical spruce-fir. This was a very cold site adjacent to the meadows on the banks of the Little Pend Oreille River.

DISCUSSION

Though we did not find nests, we did find Boreal Owls in northeastern Washington in their favored habitat during all seasons of the year. This suggests that Boreal Owls are permanent residents, in the proper habitat, in northeastern Washington. High densities occur in at least some areas; we found 12-15 birds in one area. We learned that Boreal Owls will respond to a tape of the winnowing call during most of the year. Also, we found that they were easier to locate on moonlit nights because they often approached without making a sound

Table 1. Boreal Owl record Northeastern Washington - 1985

Date	Location	Approximate Elevation	County	No. Owls	Source
27 April	Sherman Pass	1570m.	Ferry	1 seen	Bill O'Connell Bill & Geness Riechert Bart Whelton
29 April	Sherman Pass	1700m.	Ferry	2 seen	Bill O'Connell
4 May	Sherman Pass	1570m.	Ferry	0	Bart Whelton
31 May	Sherman Pass	1570m.	Ferry	0	Bart Whelton
25 June	Salmo Pass	1845m.	Pend Oreille	1 heard	Bart Whelton
1 July	Pass Cr. Pass	1645m.	Pend Oreille	0	Bart Whelton
2 July	Pass Cr. Pass	1645m.	Pend Oreille	0	Bill O'Connell Bart Whelton
3 July	Salmo Pass	1845m.	Pend Oreille	1 heard	Bart Whelton
4 July	Salmo Pass	1845m.	Pend Oreille	0	Bart Whelton
17 July	Sherman Pass	1700m.	Ferry	0	Bill O'Connell Bart Whelton
18 July	Monumental Mtn.	1580m.	Pend Oreille	0	Bill O'Connell Bart Whelton
1 Sept.	Monumental Mtn.	1580m.	Pend Oreille	1 seen	Bill O'Connell Bart Whelton
19 Sept.	Salmo Pass	1845m.	Pend Oreille	2 (1 juvenile)	Bart Whelton
28 Sept.	Colville-Kaniksu Divide	1650 to 1900m.	Pend Oreille	12 seen	Bill O'Connell Bart Whelton
19 Oct.	Kettle Crest	-----	Ferry	1 heard	Bill O'Connell Bart Whelton
15 Dec.	Tiger Highway Clark Cr. Rd.	1067m.	Stevens	3 heard	Bill O'Connell Bart Whelton

and therefore we had to depend on visual location entirely. By learning the various calls of the Boreal Owl it is possible to search for it over most of the year. Physical access to its habitat is the greatest hindrance.

Our records (Table 1) seem to support the theory advanced by Baldwin & Koplin (1966) and substantiated by Palmer & Ryder (1984) that "a contiguous breeding range extends in the Rocky Mountains from Canada south to Colorado."

Since our work by necessity was accomplished on a spare-time basis, I recommend surveys that cover a greater percentage of existing habitat both in northeastern Washington

and in spruce-fir habitats of the Cascade Mountains of Washington and Oregon. The Blue Mountains of northeastern Oregon also contain spruce-fir habitats and are also worthy of consideration.

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Home Range of Tengmalm's Owl: A Comparison Between Nocturnal Hunting and Diurnal Roosting¹

Bjørn V. Jacobsen and Geir A. Sonerud²

Abstract.--Three nesting Tengmalm's Owl males equipped with radio transmitters during a microtine rodent peak year (1985) in the northern boreal zone of southeast Norway were tracked during their nocturnal hunting, and located at their diurnal roosts, for 1-2 months. Home range sizes calculated by the convex polygon method were larger for nocturnal hunting than for diurnal roosting. The overlap between these two types of home ranges was small.

INTRODUCTION

The nocturnal behavior of owls is inherently difficult to study except in areas with continuous daylight in summer. The introduction of radio telemetry has made it possible to sample data on the activity of animals without seeing them, and to follow them continuously over large areas and long periods of time. Some of the first studies making use of radio telemetry dealt with owls (Nicholls and Warner 1972, Forbes and Warner 1974).

Tengmalm's Owls *Aegolius funereus* usually search for prey during night and roost during day (Glutz von Blotzheim and Bauer 1980). So far, their home range sizes have been calculated by either locating the owls during their diurnal roosting (Bondrup-Nielsen 1978) or by tracking the owls during their nocturnal hunting activity (Sonerud et al. 1986). However, since their habitat selection during diurnal roosting (Bondrup-Nielsen 1978, Hayward and Garton 1984) and nocturnal hunting (Sonerud et al. 1986) often differ (B.V. Jacobsen and G.A. Sonerud, unpubl.), size and shape of their home ranges calculated from diurnal roosting and nocturnal hunting may also differ. In this paper we compare these two types of home ranges by using data from three radio-equipped nesting males of Tengmalm's Owl that were tracked both during diurnal roosting and nocturnal hunting.

STUDY AREA

The study was performed during April-July 1985 within an area of 20 km² at an altitude of 480-620 m in the northern boreal zone (sensu Anonymous 1977) in Hedmark County, southeast Norway (60°55'N, 11°19'E). The study area is fairly flat and consists of Norway Spruce *Picea abies* forest with a few scattered cultivated fields. Deciduous trees, mainly birch *Betula* spp., occur sparsely. The forest structure is greatly modified by modern silviculture introduced during the last two decades, resulting in a mosaic of mostly clear-cuts and mature stands.

The study area is usually snow-covered until mid-May. In 1985 the snow-melt took place extremely late. The ground was completely snow-covered until May 8, and partly snow-covered until June 1. The snow disappeared first in the clear-cuts, and last in mature spruce forest (cf. Sonerud 1986). By May 25 the clear-cuts were completely snow-free, while snow still covered approximately half the area in mature spruce forest.

The microtine rodent prey population (e.g. Glutz von Blotzheim and Bauer 1980, Sonerud 1986) was at a peak from summer 1984 until spring 1985 (G.A. Sonerud, unpubl.).

METHODS

Three males of Tengmalm's Owl were caught in mist-net at the nest site during the nights of April 11, May 8 and June 3 1985. They were equipped with radio-transmitters (model Televilt TK-142-2S (male 1) and Biotrack SS-1), and released the same night. The three owls will be referred to as M1, M2 and M3, respectively. M1 got his transmitter replaced with a new one (same model) during the night of May 28.

¹Paper presented at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

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The three owls were tracked during their nocturnal activity for a total of 124 hours, and 59 diurnal roosts were located (table 1). The owls were never found roosting in the same tree twice or more. The nocturnal tracking was done by skiing (until May 20) or walking, cross-triangulating with a portable receiver (model Televilt RX-81) and a hand-held 4-element yagi-antenna at distances as close as possible, trying to keep in contact with the bird as continuously as possible. Tengmalm's Owls search for prey by a sit-and-wait tactic characterized by brief perchings at low heights, and do not seem to be disturbed by the observer's activity (Norberg 1970, Sonerud 1980).

When tracking the owls, locations of cross-triangulations as well as direct observations were plotted on copies of aerial photos with scale 1:15,000. Later these locations were plotted on a map with scale 1:5,000. Home range sizes were calculated for nocturnal hunting and diurnal roosting separately by the convex polygon method, i.e. the area described by connecting only the outermost locations which make a convex polygon (Mohr 1947). Both cumulative and total home range sizes were calculated.

For each owl the size and spatial distribution of the home range obtained from the nocturnal and diurnal locations were compared by calculating their overlap (O) as

$$O = \frac{2(A \cap B)}{A + B},$$

where A denotes the nocturnal home range, and B the diurnal home range, while $A \cap B$ denotes the area common to A and B (Sonerud et al. 1986).

RESULTS

The sizes of the nocturnal home ranges for the three males varied from 131 ha - 227 ha with an average of 181 ha (SD=48) (table 1). The home range sizes based on diurnal roosts varied from 94 ha - 226 ha with an average of 142 ha (SD=73) (table 1).

Table 1.--Size of and overlap between home ranges of nesting male Tengmalm's Owls based on nocturnal hunting and diurnal roosting, with number of nights (and hours) tracking the hunting owls, and number of days localizing the roosting owls. For calculation of overlap see the text.

Owl	Home-range size (ha)			Tracking effort	
	Nocturnal	Diurnal	Overlap	Nights (hours)	Days
M1	227	226	0.62	10 (54)	29
M2	184	94	0.46	13 (59)	21
M3	131	106	0.61	4 (11)	9

The overlap between the home range based on nocturnal activity and that based on diurnal roosting (fig. 1) varied from 0.46-0.62 with an average of 0.56 (SD=0.09) (table 1). For all owls the nocturnal home range was larger than the diurnal one, but the sample size is too small for statistical testing (table 1).

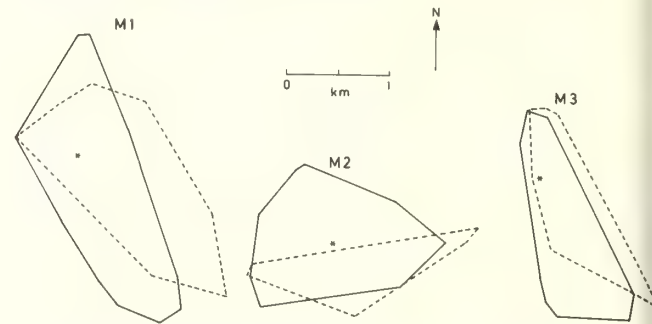


Figure 1.--Size and spacing of home ranges based on tracking the nocturnal activity (solid line) and locating the diurnal roosts (broken line) of three nesting males of Tengmalm's Owl, as calculated by the convex polygon method. Positions of nests indicated by asterices.

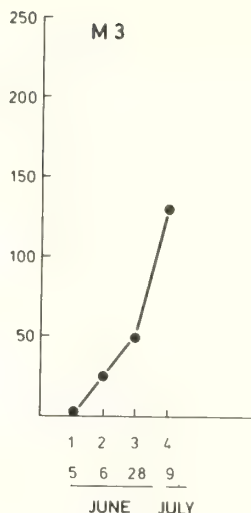
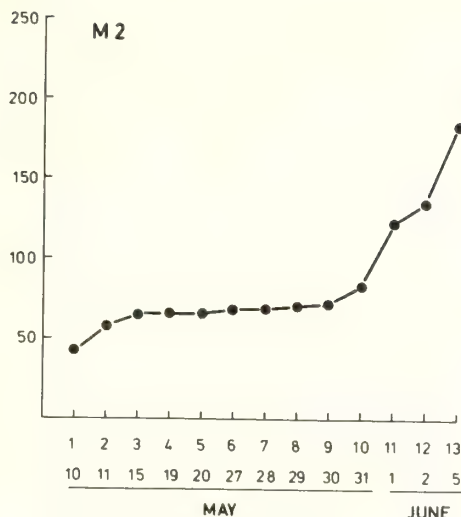
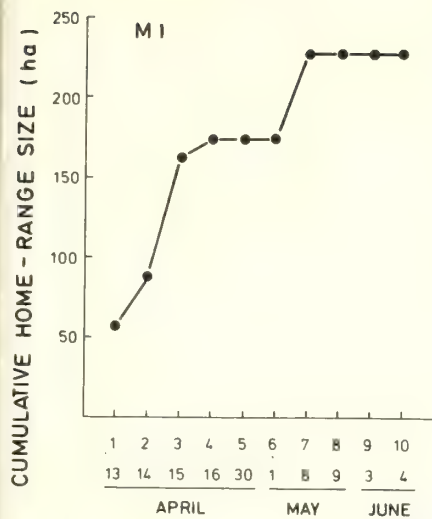
For M1 the cumulative size of both the nocturnal and diurnal calculated home range levelled off (figs. 2 and 3), thus indicating that the total sizes calculated were the real home range sizes of this owl. For M2 the cumulative size of the diurnal home range levelled off (fig. 3), while that of the nocturnal home range did not (fig. 2). Thus we probably have underestimated the real nocturnal home range size, but possibly have correctly estimated the diurnal home range size, of this owl. For M3 neither of the cumulative sizes levelled off during our study (figs. 2 and 3), indicating that both the nocturnal and the diurnal home range sizes calculated are underestimations of the real home range sizes of this owl.

DISCUSSION

Reliability of the calculated home range sizes

The cumulative size of the nocturnal home range levelled off for one male (10 nights of tracking), but not for the two others (4 and 13 nights). Sonerud et al. (1986) suggested that more than five nights of tracking are needed to reveal the actual nocturnal home range size of a nesting male Tengmalm's Owl. Our data indicate that even more than 13 nights may be needed. Similarly, the cumulative home range size of 3 Eastern Screech Owls *Otus asio* in Connecticut, USA, continued to increase throughout the time monitored (Smith and Gilbert 1984).

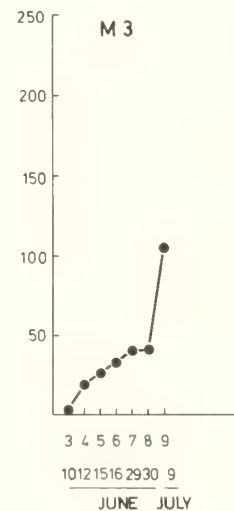
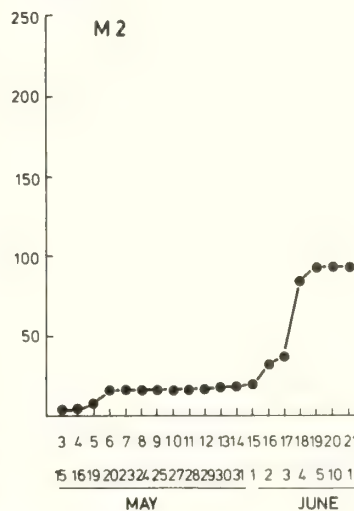
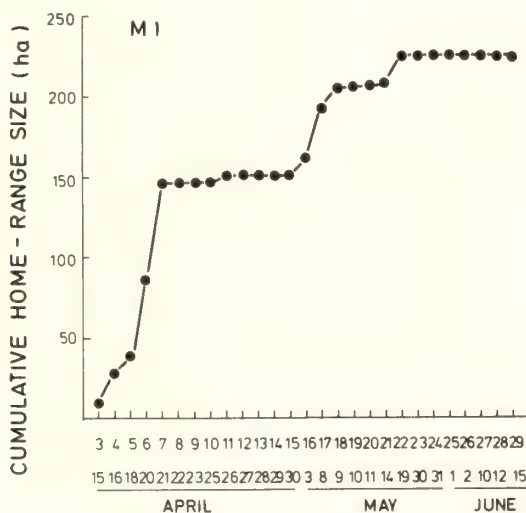
The cumulative size of the home range based on diurnal roosts levelled off for two males (21 and 29 days of locating), but not for the third (9 days). Therefore, in order to obtain the



NUMBER OF NIGHTS TRACKED (DATE)

Figure 2.--Cumulative size of nocturnal home range in relation to number of nights tracking for three nesting males of Tengmalm's Owl, as calculated by the convex polygon method. Dates of days succeeding the tracking nights are shown.

Figure 3.--Cumulative size of diurnal home range in relation to number of days locating the diurnal roost for three nesting males of Tengmalm's Owl, as calculated by the convex polygon method. Dates of days locating are shown.



NUMBER OF DAYS TRACKED (DATE)

real diurnal home range size, the diurnal roost should probably be located on at least 10 days, but not necessarily more than 20.

Home range size in relation to ecological factors

We know of only one former study of nocturnal home range size in the Tengmalm's Owl. A male tracked for five nights in an area neighbouring our study area had a recorded home range size of 205 ha (Sonerud et al. 1986). This is within the range found in our study, but is rather large when the few nights of tracking are corrected for. The rather large home range may have been caused by the lower prey availability in the study of Sonerud et al. (1986) than in our study. In Canada three nesting males of the sub-

species Boreal Owl *Aegolius f. richardsoni* were found to have home ranges of 100 ha, 250 ha and 500 ha, calculated from the locations of their diurnal roosts only (Bondrup-Nielsen 1978). A male of the related Saw-whet Owl *Aegolius acadicus* studied over twenty days in late autumn in Minnesota, USA, had a home-range of 227 ha, as calculated by the convex polygon method from data in Forbes and Warner (1974).

The availability of prey for Tengmalm's Owls in clear-cuts strongly increases from snow-covered to snow-free ground in spring (Sonerud 1986), while it decreases during summer due to growth of field vegetation (Sonerud et al. 1986). M2 spent almost all his hunting effort in the large clear-cut surrounding his nest during snow-melt and the first week after the snow had

disappeared in the clear-cut. Both nocturnal and diurnal cumulative home range size levelled off during this period. By the end of May when the early growth of field vegetation had made prey less available in the clear-cut, M2 started spending more time hunting in the mature spruce forest stands, and the size of the home range increased. However, this increase also coincided with the female's resuming of hunting after incubation and brooding. Therefore, both lowered prey availability in the clear-cut as well as avoidance of overlap with the female's hunting area may explain the increase of the home-range size. The small home range size of M2 at the time when the female resumed hunting was due to the clear-cut being a core area (cf. Samuel et al. 1985), with a high availability of prey during snow-melt. For M1, the home range did not include any such high prey availability core area, and had thus reached its final size by the time the female resumed hunting. Therefore, no further increase occurred when both mates exploited the home range.

Nocturnal and diurnal home ranges: Which should be measured?

For all three males there was a relatively small overlap between the nocturnal and the diurnal home range. This was independent of the number of nights the owls were tracked and the number of roosts located. The overlap was smaller for M2 than for the two others. M2 nested in a box situated in a 20 ha clear-cut (see description in Sonerud (1986)), and his home range included few middle-aged stands of Norway spruce, which we found the Tengmalm's Owl to prefer as roosting habitat (B.V. Jacobsen and G.A. Sonerud, unpubl.). This may explain why the home range based on diurnal roosts, and hence why the overlap between the nocturnal and diurnal home range, were so small for this male. For the two other males, the middle-aged stands preferred for roosting were more common throughout the home range.

Smith et al. (1981) found that the diurnal home ranges of coyotes *Canis latrans* in general were included in the nocturnal home ranges. This would also have been the case in the Tengmalm's Owl if we had tracked the males until they roosted each night, and not located their roosts separately. However, in our study several roosts were located at days when the owl had not been tracked the night before. This explains why the diurnal home range is not included in the nocturnal home range for any of the three males. Hence, we conclude that tracking the owls during their nocturnal hunting until they have roosted will be sufficient to give a reliable estimate of the real home range size, while home range sizes based on diurnal roosts only will be underestimations of the real ones.

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The Breeding Biology of Northern Saw-Whet Owls in Southern British Columbia¹

Richard J. Cannings²

Abstract.-- A study of 12 Northern Saw-whet Owl nests over three years in two distinct habitats yielded data on nesting chronology, clutch size, nestling growth, nesting success and prey selection. Radio telemetry data provided information on the movements of three males and two fledglings.

INTRODUCTION

The Northern Saw-whet Owl (*Aegolius acadicus*) is a relatively common and widespread owl, breeding across North America from central Canada south to central United States (Godfrey 1986). Despite its extensive range throughout populated North America, little is known of its breeding biology. I became interested in saw-whets in 1984 when I found three nests in 30 nest-boxes put up for Flammulated Owls in the Okanagan Valley of south-central British Columbia (fig. 1). That winter I put up over 150

nest-boxes hoping to attract a proportionate number of owls, but the boxes still held only three pairs of saw-whets in both 1985 and 1986. In 1986 I also found two nests in natural cavities.

Northern Saw-whet Owls breed in two distinct habitats in the Okanagan Valley: montane coniferous forests and riparian deciduous woodlands. In the montane coniferous forests, by far the most abundant habitat in the region, they are found up to 1400 m elevation, but are commonest from 500 to 1000 m where ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) predominate (hereafter called the "pine-fir forest"). Saw-whets are occasionally seen above 1500 m elevation, but seem to be replaced as a breeding species above this altitude by the larger Boreal Owl (*Aegolius funereus*). The deciduous woodlands are characterized by stands of water birch (*Betula occidentalis*) along old oxbows of the Okanagan River, surrounded by wet meadows and pastureland at 280 m elevation. This habitat is very restricted in the Okanagan Valley, with an area of less than 1000 ha. One focus of my study was to compare the breeding ecology of saw-whets in these two different habitats, but the work was initiated primarily to gather some basic breeding biology data on this species.

STUDY AREA AND METHODS

I was unable to find any nests in pine-fir forests in 1985, when I concentrated my efforts in monitoring 100 nest-boxes in a 4200 by 600 m grid near Naramata, northeast of Penticton. In 1986, therefore, I looked throughout the south Okanagan area for singing males in March and April and concentrated nest searches around the birds I found. That year I succeeded in finding two nests in this habitat, both in natural cavities (fig. 1, Penticton and Okanagan Falls sites). The road survey for singing males also provided a rough measure of the relative population densities of saw-whets in the two habitats.

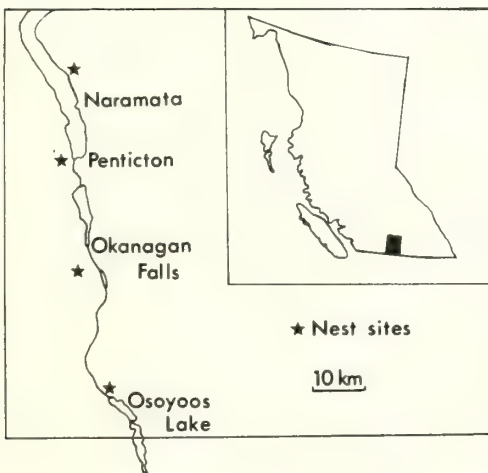


Figure 1.--Okanagan Valley study area; inset shows position in British Columbia.

¹Paper presented at the symposium, Biology and Conservation of Northern Forest Owls, February 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

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I had better luck with finding nests in the more restricted deciduous woodland habitat. In January 1985 I essentially filled the available habitat (about 65 ha of woodland) in the 235-ha Osoyoos Oxbows Wildlife Reserve with 63 nest-boxes in addition to the 10 Wood Duck boxes already there. Three pairs used these boxes in both 1985 and 1986; I found no nests in natural cavities in this habitat.

I visited nests every two to three days, except during incubation when visits were less frequent. I weighed nestlings to the nearest gram with a Pesola spring scale and measured their wing chord, culmen, head, tail, and tibiotarsus length with dial calipers.

Whole or half-eaten prey were commonly found in nests from the egg-laying period through the early nestling period. I identified, sexed, and measured all prey remains at each visit. As the nestlings grew, fewer uneaten prey items were found in nests, and the brooding females kept the nests free of pellets and droppings. When the youngest nestling was about 15 to 18 days old, however, the females stopped brooding the young and a considerable quantity of pellets and other prey remains built up in the nests. After the young left the nests, I removed and examined the nest material for these prey remains. Small mammal prey from this material were generally identified by examining the lower jaws, since the skulls were destroyed in most cases.

I trapped and banded all eight adult females and most (8 of 10) adult males, measured them, and marked their facial disks with waterproof ink for individual recognition. In addition, I put a colored plastic jess on all birds in 1985 and on three adult females in 1986, but two of the six females removed the jess quickly so I stopped the practice. I trapped adult females on their nests and mist-netted adult males in front of the nests; I also noosed two unpaired males on their day-roosts.

To get an estimate of prey density and diversity, I trapped small mammals in two different ways. In 1985 I live-trapped and marked mice in Longworth traps set 10 m apart in grids at the Osoyoos site (39 traps, 6 nights) and at the Naramata site (100 traps, 3 nights). In 1986 I snap-trapped small mammals once a month from March through June (50 traps set 5 m apart in a line through representative habitats) at the Penticton and Osoyoos sites.

Late in the 1986 breeding season, I was able to attach 3-gm radio transmitters (Lotek Engineering, Aurora, Ontario) to two breeding males (feeding nestlings and fledglings; one each at Penticton and Osoyoos), one non-breeding male, and two fledglings (one each at Penticton and Osoyoos) to monitor their movements and locate roosting sites. I tracked these birds by following them on foot with a hand-held, two-element yagi antenna and portable receiver, and calculated home ranges by the convex polygon method.

RESULTS

Population Densities

In 1986, 21 singing male saw-whets were heard on 104 km of surveys through the pine-fir forests (0.2/km), while 5 were heard on 10 km of surveys through the deciduous woodland habitat (0.5/km). This indicates that the Northern Saw-whet Owl population in the deciduous woodland may be about 2.5 times as dense than that in the pine-fir forests, although this figure is obviously imprecise.

Nest Sites

Of twelve nests found in this study, ten were in nest-boxes. Eight of the nest-boxes were approximately 43 x 18 x 18 cm, one was approximately 60 x 25 x 25 cm, and the last was 30 x 15 x 15 cm in size. These boxes were nailed to tree trunks from 2.6 to 6.1 m above the ground. The two natural sites were in Northern Flicker (*Colaptes auratus*) holes in old ponderosa pine snags 2.8 and 4.6 m above the ground. Nearest neighbour distances between nests at the Osoyoos site ranged from 0.8 to 1.4 km (mean 1.1 km, $n=4$).

Site Fidelity

In 1985, all the females and two of the males from the three nesting pairs were banded at Osoyoos, as well as an unpaired male and all of the fledglings. In 1986, three pairs at least attempted to breed on the area, as well as another unpaired male. None of the females were the same as the previous year, and at least two of the breeding males were new. The third breeding male and the unpaired male were not caught in 1986, but I could not see bands on their legs despite close views. From this small sample, it would seem that Northern Saw-whet Owls are not strongly philopatric. Interestingly, one of the 1986 pairs nested in the same box (out of 25+ to choose from on their territory) in which a totally different pair nested in 1985.

Nesting Phenology

Northern Saw-whet Owls begin nesting in the Okanagan Valley in March. Nine clutch initiation dates ranged from 1 to 31 March, with a mean of 12 March. The exact timing of clutch initiation may be weather-related; the earliest nest at Osoyoos was started 12 days earlier in 1986, when there was a sudden amelioration of daily mean temperature in late February, than in 1985, when the amelioration was more gradual. Comparisons between the two habitats can only be made for 1986, when clutches were initiated at Osoyoos (280 m el.) on 1 and 5 March, while clutches at Penticton (550 m) and Okanagan Falls (615 m) were initiated on 8 and 21 March respectively.

One 1984 nest at Naramata begun about 16 May was probably a second clutch, especially considering that a second nest about 1 km away (perhaps belonging to the same female?) fledged its last young on 17 May.

The earliest nest, begun on 1 March 1986 at Osoyoos and containing a full clutch of five eggs on 10 March, was abandoned on the latter date due to disturbance at the nest. Two days later the same female began laying a replacement clutch in a nest-box 270 m away and completed another clutch of five eggs, thus laying 10 eggs in a 21-day period. Laying, hatching and fledging intervals and incubation and nestling periods are summarized in table 1.

Incubation may sometimes begin with the second egg laid, since the two instances of an incubation period (calculated from the day an egg was laid) greater than 27 days both concerned the first young to hatch in a nest.

Table 1.--Nesting intervals and periods. Sample sizes are for individual eggs or nestlings.

	n	Range (days)	Mean
Laying Interval	7		2.0
Incubation Period	9	27-29	27.3
Hatching Interval	19		1.7
Nestling Period	12	29-36	33.4
Fledging Interval	9		1.4

Clutch Size and Nesting Success

The clutch size of nine nests ranged from five to seven, with a mean of 5.9 eggs and a mode of six (four nests). This value is somewhat larger than those given in Murray (1976).

Excluding two nests which were almost certainly abandoned due to human disturbance, I could calculate nesting success parameters from seven nests, summarized in table 2. Hatching failures were due to infertile eggs or the death of embryos in eggs; no nests (other than the two mentioned above) were abandoned or predated in the egg stage. Interestingly, the two cases of major hatching failure (five of six and three of five eggs failing) involved the probable second clutch and the definite replacement clutch (see above).

The causes of nestling deaths were harder to determine. Four nestlings in one brood of six died within two days of hatching, apparently from an infestation of *Carnus hemapterus*, a small blood-sucking, parasitic wingless fly found in the nests of hole-nesting and raptorial birds (Cannings 1987). The other two nestlings in this nest were near fledging when I found them dead on the ground below the nest-box with a male Northern Flicker roosting in the box. Nestlings at the

Table 2.--Northern Saw-whet Owl nesting success.

Mean Eggs Laid	Mean Clutch Size	Mean Eggs Hatched	Mean Brood Size	Mean Young Fledged	Mean No. Fledged	Over- all Success
40	5.7	30 75%	4.3	17 56%	2.4	42.5%

Okanagan Falls site disappeared one by one for no apparent reason. Whole prey remains were plentiful in the nest and no ectoparasites were found in the nest or on the young; the only cause for failure I can think of is the female failing to brood and/or feed the young properly. The two youngest nestlings in another nest were apparently killed and partially eaten by their siblings just before fledging.

Nestling Growth

Young Northern Saw-whet Owls are born with eyes closed and with a covering of white down. By day 5 dark tracts of developing pin-feathers are visible dorsally, becoming very evident by day 7. The eyes open between day 7 and 10, and the nestlings begin bill-snapping at intruders at about the same time. The egg-tooth is lost around day 10, and by day 13 or 14 the primary sheaths begin to split.

The weight gain of nestlings is illustrated in figure 2. Weight gain is essentially linear (7 gm/day) from about day 4 to 14, then tapers off and reaches an asymptote at about 3 weeks of age. The large variation in weights from day 11 to 22 is due to two slow-growing nestlings which eventually died before fledging. After reaching about 100 gm, the weights of nestlings can fluctuate widely from day to day, but the mean weight of all nestlings is fairly constant until fledging. Nestlings usually lose weight after four weeks of age; the mean maximum weight of 12 nestlings was 111.0 gm while their mean fledging weight was 95.9 gm (table 3). Growth of the wing chord is essentially linear (3.9 mm/day after primary feather development starts at about day 7, and only slows slightly before fledging (fig. 3). A juvenile measured at 58 days of age had a wing chord of 131 mm, well within the adult range.

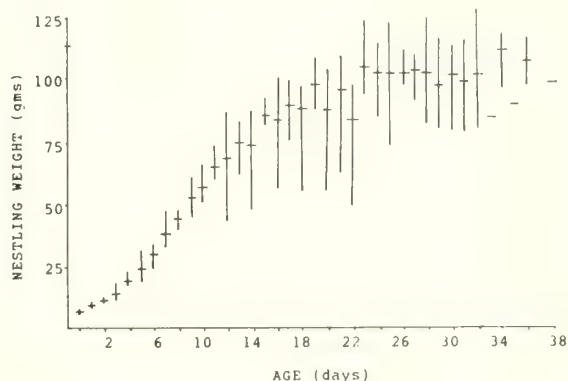


Figure 2.--Nestling weight vs. age; vertical bars are ranges, horizontal bars are means.

Table 3.--Maximum and fledging weights of nestlings from Osoyoos (deciduous woodland) and Penticton (pine-fir forest) nests.

		Maximum Weight		Fledging Weight (gms)	
	n	Range	Mean	Range	Mean
Osoyoos	6	95-123	106.5	77.5-103	86.6
Penticton	6	111-127	115.5	96-115	105.2

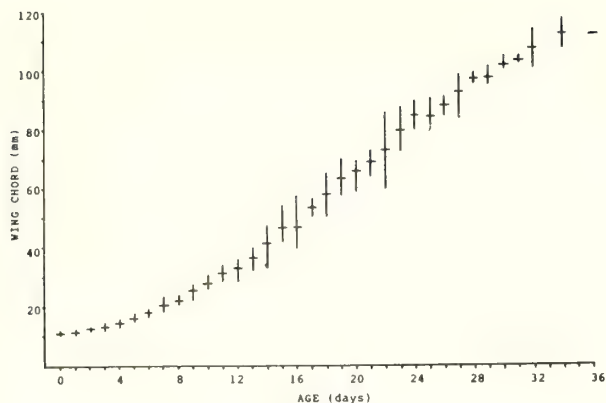


Figure 3.--Wing growth of nestling Northern Saw-whet Owls.

Home Ranges

The calculated home range sizes of the two nesting males at Osoyoos and Penticton were 142 and 159 ha respectively (figs. 4 and 5). These values are based on 21.5 hrs of radio tracking at Osoyoos and 17.5 hrs at Penticton. For 18.5 hrs of the 21.5 hrs he was monitored, the Osoyoos male stayed within a core area (approximately 27 ha) of his range, but the Penticton male regularly covered most of his home range.

Prey Densities

The results of the small mammal trapping are summarized in figure 6. Traps set in pine-fir forests caught only northwestern chipmunks (*Tamias amoenus*), deer mice (*Peromyscus maniculatus*), and one long-tailed vole (*Microtus longicaudus*); I considered the chipmunks to be too large and

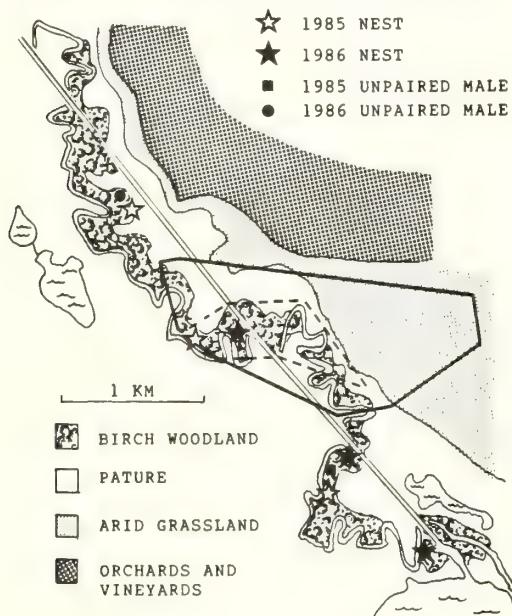


Figure 4.--The Osoyoos study area. Heavy solid line outlines the home range of male radio-tracked in 1986; dashed line outlines core area of male's home range.

diurnal to be saw-whet prey and eliminated them from the analysis. The samples from the Osoyoos area were much more diverse and indicated a prey density of at least four to five times that found in the pine-fir forests.

Diet

The analysis of prey remains found in nests and at roosts is summarized in table 4 and compared with

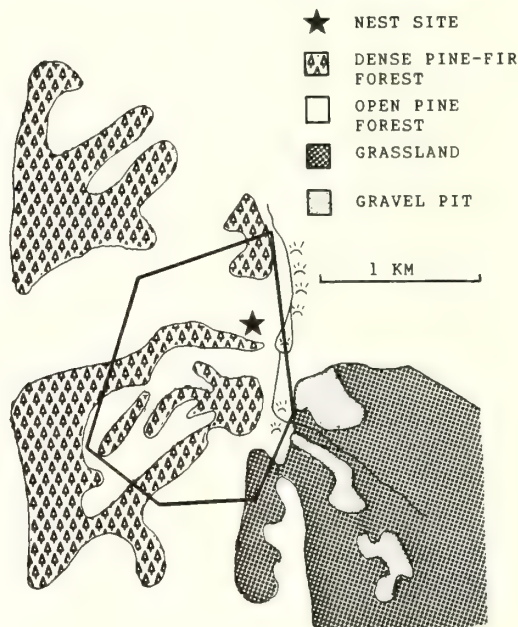


Figure 5.--The Penticton study area. Heavy solid line surrounds home range of male.

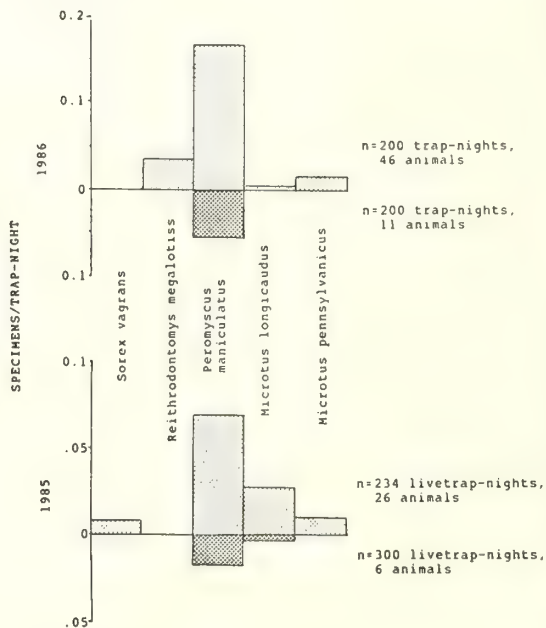


Figure 6.--Prey availability from trapping results. Light stippling: deciduous woodlands at Osoyoos; heavy stippling: pine-fir forests at Penticton and Naramata.

Table 4.--Diet of Northern Saw-whet Owls in the Okanagan Valley.

SPECIES	Weight (gm)	DECIDUOUS WOODLANDS				PINE-FIR FORESTS			
		No.	%	Total Weight	% Weight	No.	%	Total Weight	% Weight
Insects	---					6	2.3	---	---
Birds	19.4 ¹	4	1.2	77.6	1.0	5	1.9	97.0	1.9
<u>Sorex cinereus</u>	4.1 ²					1	.4	4.1	.1
<u>S. vagrans</u>	7.2 ²	8	2.4	57.6	.8				
<u>Sorex spp.</u>	5.0 ³					2	.8	10.0	.2
<u>Perognathus parvus</u>	18.3 ⁴	85	26.0	1555.5	20.4	3	1.2	54.9	1.1
<u>Reithrodontomys megalotis</u>	10.9 ⁴	13	4.0	141.7	1.9	6	2.3	65.4	1.3
<u>Peromyscus maniculatus</u>	19.5 ⁴	119	36.4	2320.5	30.5	217	84.4	4231.5	83.7
<u>Microtus spp.</u> ⁵	35.3 ⁴	98	30.0	3459.4	45.4	16	6.2	564.8	11.2
<u>Clethrionomys gapperi</u>	27.5 ²					1	.4	27.5	.5
TOTALS		327		7612.3		257		5055.2	

¹Mean weight from Dunning (1984) of four bird species found in saw-whet nests.

²Weight from Banfield (1974).

³Weight estimated from Banfield (1974).

⁴Mean weight of this species from specimens collected in the study area.

⁵Includes Microtus longicaudus, M. montanus, and M. pennsylvanicus.

estimates of prey density in figure 7. It is clear that Peromyscus maniculatus is the favoured prey in the pine-fir forests, not surprising considering the results of the small mammal trapping there. Deer mice, voles (Microtus spp.), and Great Basin pocket mice (Perognathus parvus) were about equal in numbers in the Osoyoos sample, although voles were most important when the mean weight of prey was considered. Voles predominated in early samples (March and early April), while pocket mice were rare in March but common in April samples (fig. 8). Wandering shrews (Sorex vagrans) and migrant passerines (Yellow-rumped Warbler, Dendroica coronata; White-crowned Sparrow, Zonotrichia leucophrys; Lincoln's Sparrow, Melospiza lincolni) formed a minor part of the diet at Osoyoos. In pine-fir forest habitat minor diet constituents included common shrews (Sorex cinereus), Great Basin pocket mice, long-tailed voles, meadow voles (Microtus pennsylvanicus), montane voles (M. montanus), birds (Dark-eyed Junco, Junco hyemalis; Pine Siskin, Carduelis pinus), and a few insects. The latter were found in pellets under a roost of an unpaired male.

DISCUSSION

Although the effects are not always apparent in my small sample of nests, it is clear that the pine-fir forest and deciduous woodland are markedly different habitats for Northern Saw-whet Owls. Beyond the obvious structural differences of the vegetation itself, which affect the availability and quality of roost and nest sites, the main difference is in the availability of prey. Small mammal population densities are

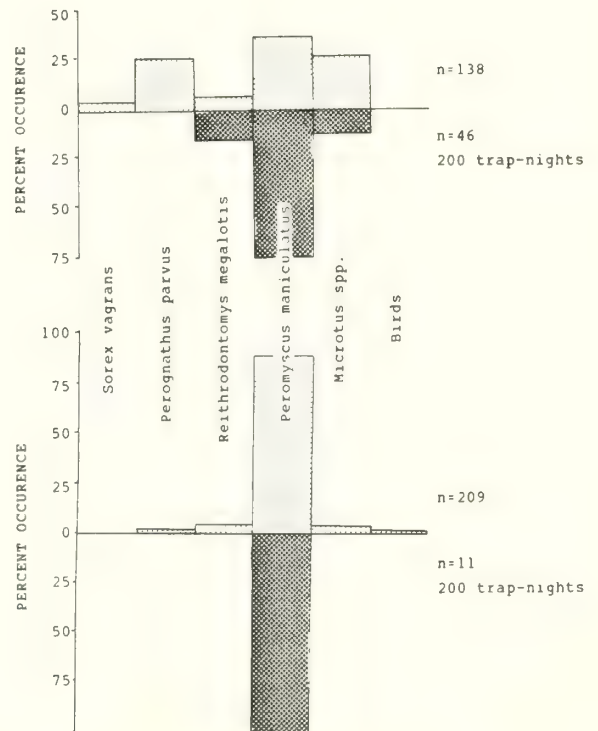


Figure 7. Comparison of 1986 prey density estimates (heavy stippling) and prey remains at nests (light stippling). Top: Osoyoos deciduous woodlands; bottom: Penticton pine-fir forests.

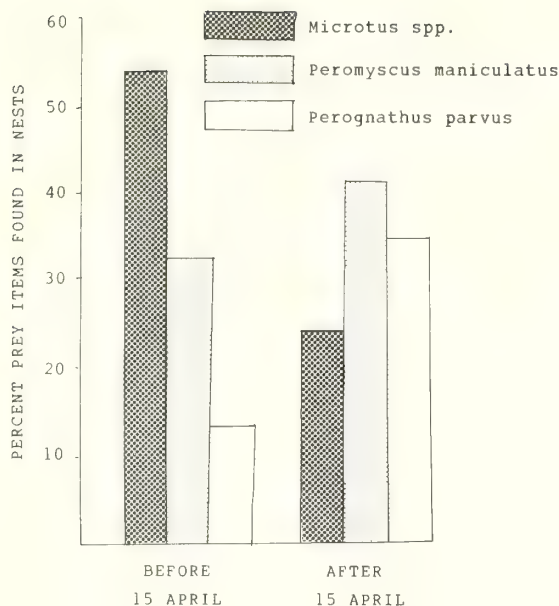


Figure 8.--Relative abundance of voles, deer mice, and pocket mice in nests at Osoyoos in early and late spring.

obviously larger in the deciduous woodlands, and prey species diversity is greater there as well. High prey species diversity would be an advantage if one prey species declines in numbers while others remain high. The dependence of saw-whets on *Peromyscus maniculatus* was also noted by Palmer (1986).

A confounding factor in the prey density equation is the presence of other mouse-eating raptors in the study areas. The Osoyoos area, for instance, supported at least nine pairs of Long-eared Owls (*Asio otus*) and one pair of Great Horned Owls (*Bubo virginianus*) in the woodlands and two pairs of Burrowing Owls (*Athene cunicularia*) on the adjacent grasslands, plus several Red-tailed Hawks (*Buteo jamaicensis*) and Northern Harriers (*Circus cyaneus*). All of these species could conceivably compete with saw-whets for small mammal prey, although none of them take *Peromyscus maniculatus* to any extent.

Considering the prey data and the estimated relative population densities calculated for the two habitats, I was somewhat surprised by the small difference in the calculated home range sizes (142 vs. 159 ha) for the Osoyoos and Pentiction males, but the smaller core area used by the Osoyoos male helps explain this apparent similarity. More radio telemetry work is needed to determine if these home range sizes are accurate and representative. These areas are larger than the 114 ha reported for a saw-whet tracked for 20 days in November in Minnesota (Forbes and Warner 1974), but only about half of the mean of 296 ha found for Boreal Owl home ranges in Colorado (Palmer 1986).

My sample sizes are too small to detect meaningful differences in nesting success and

nestling growth between saw-whets in the two habitats. Further work will hopefully result in more accurate measures of these parameters as well as better prey availability estimates. The shifts in prey taken through the breeding season at Osoyoos are interesting. The high number of voles taken early in the season may indicate that voles form the bulk of the winter diets of Northern Saw-whet Owls, as Catling (1972) found in Ontario. Vole populations are generally high throughout the winter, then drop sharply in early spring (Krebs and Boonstra 1978). The shift to *Perognathus parvus* is easier to explain, since this species hibernates all winter, and "few are seen between November and March" (Banfield 1974, p. 154).

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Study of a Northern Saw-Whet Owl Population in Sauk County, Wisconsin¹

Scott R. Swengel and Ann B. Swengel²

We censused a population of Northern Saw-whet Owls (*Aegolius acadicus*) in 1986 in southern Wisconsin, using the spot-mapping method. Saw-whet Owls called voluntarily from 21 February to 27 April, and last responded to taped calls on 14 May. Their detectability was high in March and dropped considerably in April. Auditory censusing in March and April using tape-recorded calls yielded 18 Saw-whet Owls along a 7.2-km survey route. Population density was 5.0 singing Saw-whet Owls/km²; one 116-hectare area had a density of 12.9 singing Saw-whet Owls/km². We surveyed most of this route for Eastern Screech-Owls (*Otus asio*) with tape playback. The distribution of Saw-whet Owls and Screech-Owls was remarkably disjunct, with only slight overlap of these species; this segregation was statistically significant ($P < .001$). Saw-whet Owls occurred in large tracts of forest, including pine plantations, whereas Screech-Owls occupied forests near open areas. We noted 11 instances of interspecific call answering to tape playback by these two species. Pellets of Saw-whet Owls were measured and their contents analyzed. Roost sites of Saw-whet Owls were adapted to the different sizes, growth habits, and canopy of each tree species.

DESCRIPTION OF STUDY AREA

We studied a population of Northern Saw-whet Owls (*Aegolius acadicus*) from February to December 1986 in the Baraboo Hills of Sauk County, Wisconsin. The Baraboo Hills are a range of bluffs and hills up to 150 m above the surrounding terrain in Sauk and Columbia Counties, Wisconsin. Although the Baraboo Hills are south of the tension zone between northern mixed hardwood-coniferous forests and southern deciduous forests and prairies, several northern forest types are found here and Mossman and Lange (1982) state that "...a typical forest in the Baraboo Hills might best be described as intermediate between northern and southern types" (p. 19). White pine is-lands grow on the exposed talus slopes and cliffs, jack pine-oak barrens on the infertile sandy areas, southern oak hardwoods in the flatter, lower areas, upland forests dominated by oak (a southern forest type) or maple (a northern forest type) in the drier areas, with northern communities in the stream gorges and rocky bluffsides. Pine plantations are scattered throughout the area.

Our four study areas are Baxter's Hollow, a stream gorge in the western Baraboo Hills; Devil's Lake State Park south shore area, a rugged area containing all the communities discussed above except pine barren; Steinke Basin in Devil's Lake State Park, a basin with wet meadow and prairie with deciduous oak forest and pine plantations on the perimeter; and Mirror Lake Pine Barren, immediately north of the Baraboo Hills, a jack pine-oak-red cedar barren with dry prairie. Immediately around the pine barren are pine plantations and oak hardwood forests. The study sites are located at 43° 23' to 43° 34' N and 89° 41' to 89° 49' W, and vary from 270 to 450 m in elevation.

The Eastern Screech-Owl (*Otus asio*) is a resident breeder in agricultural, urban, and woods-edge habitat in the Baraboo Hills, while the Saw-whet Owl is considered a possible breeding bird (Mossman and Lange 1982). Follen (1981, 1982) has reviewed the status of Saw-whet Owls in Wisconsin and found only one nest record at or south of the latitude of our study area during the 20th century: 11-27 July 1953, Milwaukee County, 4-5 eggs in the nest, reported by Schwendener in the *Passenger Pigeon* 15: 178 (1953) (as cited by Follen 1981).

METHODS OF DETECTING OWLS

Our first method of detecting owls was listen-

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ing for voluntary calling. At dusk we selected a listening station and sat there motionless for the duration of the observation period. It was important to arrive before the owls began calling, not only to record that fact but also because it appeared to disturb them if we moved in their vicinity after calling began but before it was fully dark. We recorded the beginning and ending time each time an owl called as well as the direction from us to the owl's calling station. Absolute silence greatly increased the number of vocalizations we heard.

Our second method, auditory censusing with tape-recorded calls, used the strip transect method of censusing (Ralph 1981). We spot-mapped the calling records as Emlen (1984) did in censusing songbirds. For Saw-whet Owls, we used a calling tape which consists of ten 40-second sequences of the Saw-whet Owl song as recorded on "Voices of New World Nightbirds" (ARA Records, Inc.; available from the Laboratory of Ornithology, Cornell University, Ithaca, New York, USA) separated by a blank section of tape, and listening stations spaced 100 m apart. In one later census we used 200 m intervals between listening stops to increase our efficiency. Using a portable cassette recorder and starting after nightfall, we played 20 seconds of song, paused to listen, played the remaining 20 seconds of song, and paused again to listen.

For Eastern Screech-Owls, we used a calling tape of 12 monotone (trill) songs of the species as recorded on "A Field Guide to Bird Songs of Eastern and Central North America" (Cornell Laboratory of Ornithology, Ithaca, New York, USA), and listening stations spaced 200 m apart. Using a portable cassette recorder and starting after dark, we played 3-4 songs, paused to listen, played 3-4 more songs, and paused again to listen. During every census, we recorded any response by any species of owl, describing the vocalization, the direction of the calling station relative to us, the duration of the vocalization, and any other relevant observations.

Our third method of detection was visual location during the day. From February to December, we systematically searched locations in the four study areas for fecal wash and pellets of Saw-whet Owls. During these searches we looked for roosting Saw-whet Owls. When we located a Saw-whet Owl, we quickly recorded its roost data and behavior and then left the vicinity. When sufficient fecal wash was present to identify the location of the roost, its height, its distance from the trunk, the length of the roost branch, and the tree species were noted. The height and diameter at breast height (dbh) of roosting trees were also recorded. Pellets were collected regularly from roosting areas and were analyzed individually; they were soaked in 0.03 molar NaOH for 1-4 days or simply picked apart.

RESULTS OF DETECTING SAW-WHET OWLS

We initiated listening sessions for voluntary calling of Saw-whet Owls on 21 February and discontinued on 7 March 1986, with attempts on nine nights, all in the same area in Devil's Lake State

Park, south shore near stop 19 (fig. 1). We began listening before sunset and the observation period lasted 22 to 62 minutes. On the six nights in which winds were less than 15 km per hour, we heard at least one owl (Swengel and Swengel 1986). With this method, we found 5 owls, numbered 8-12. In addition to our observations, we received 4 records of voluntary calling from another competent observer. Saw-whet Owls called voluntarily from 21 February to 27 April. However, they had probably begun calling earlier, since we heard voluntary calling on the first night in which we listened for it. K. Lange (pers. comm.) has heard voluntary calling in our study area as early as 10 February.

We censused Saw-whet Owls with tape-recorded calls in three of the four study areas. At Devil's Lake, south shore area, where most surveying occurred, the strip transect consisted of 75 stops spaced 100 m apart along two transects that intersected. One transect (stops 1-56) was 5.5 km long and the other (stops 57-75) was 1.7 km long (fig. 1). Stops 13-56 were surveyed for Screech-Owls and stops 1-75 were surveyed for Saw-whet Owls. Because the Saw-whet calling period was so short, we concentrated our censusing in the densely populated western end of the Devil's Lake survey area, where repeated censusing was necessary to determine how many Saw-whet Owls were present. Consequently, other listening stations were censused only once or twice. Baxter's Hollow was also surveyed for both species and Steinke Basin for Saw-whet Owls only. Saw-whet Owls responded to tape playback on the first census on 9 March and continued to respond until 14 May. Auditory censusing in March and April using tape-recorded calls of Northern Saw-whet Owls yielded 17 Saw-whet Owls, numbered 1-13 and 15-18, along the 7.2-km survey route. Auditory censusing from March to May in the Steinke Basin and Baxter's Hollow yielded six more owls, numbers 19 and 21-25. Two additional owls, number 14 at Devil's Lake south shore and number 20 at Baxter's Hollow, were only observed by us to respond to the Eastern Screech-Owl tape, although another competent observer documented response by number 20 to a Saw-whet Owl tape.

The ease with which we found wash, pellets, and/or owls--i.e. the success of visual location during the day--varied considerably. Saw-whet Owl 22 was seen on seven days from 17 March to 4 November, and heard once during the day on 23 March. Owl 24 was sighted once on 30 March. Eastern Screech-Owl E or F was heard during the day on 29 March. On 21 additional days, fecal wash and/or pellets of Saw-whet Owls were located. Attempts were made on at least nine additional days. Pellet and roost analyses are discussed later.

DISCUSSION OF DETECTION METHODS

Each of the three methods of detection has advantages and disadvantages. Visual detection is the slowest and most time-intensive, and probably never will yield an accurate census of Saw-whet or Eastern Screech-Owls. Certainly, the history of observations of Saw-whet Owls and, to a lesser extent, Eastern Screech-Owls in the Baraboo Hills did not

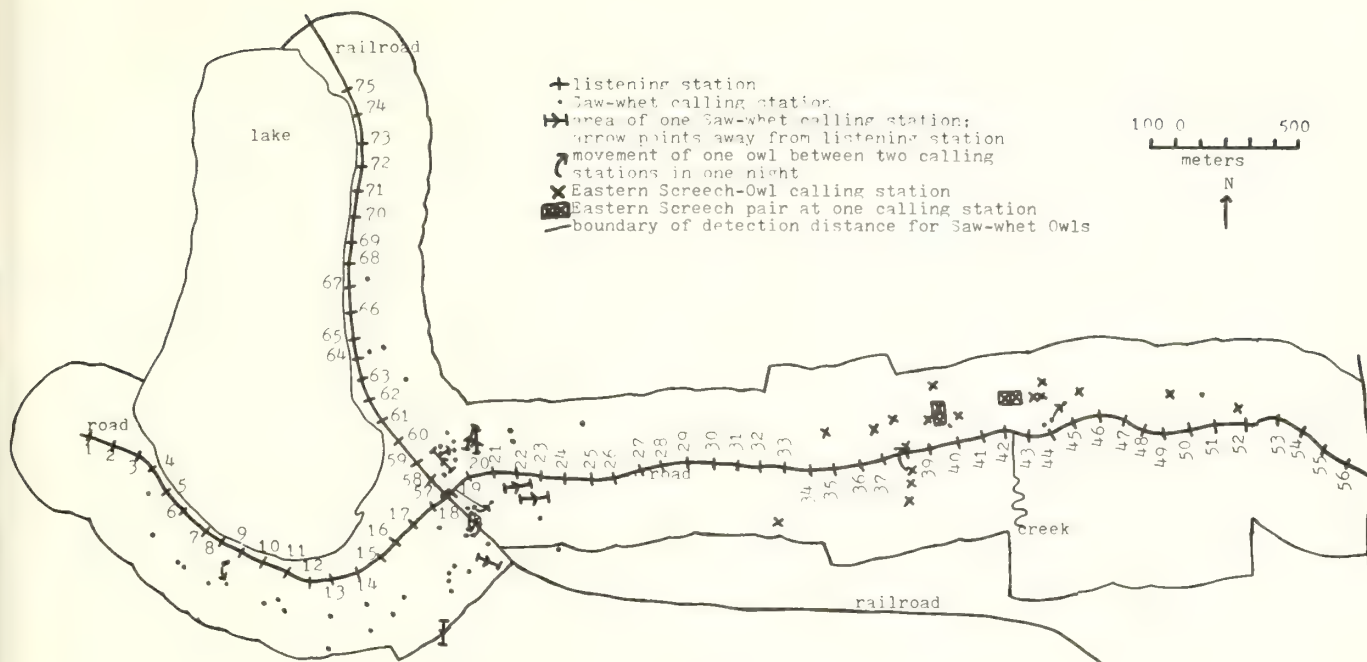


Figure 1. Map of Devil's Lake State Park, south shore area and Steinke Basin, showing the census route, numbered listening stations, area in which Saw-whet Owls were detectable, and the calling records of different Saw-whet Owls and Eastern Screech-Owls.

prepare us for the results we obtained with the other two methods. However, visual searching is the only way to study pellets and roost site selection. Furthermore, in the absence of vocalizations--and the Saw-whet Owl in particular is very seasonal in vocal response--visual detection is the only realistic method of detection. However, at the same time that it becomes difficult to elicit vocal responses, it also becomes more difficult to find pellets and roosts. We believe the warmer weather and presence of hungry invertebrates erases the evidence quickly. Many pellets we collected during the late spring and summer contained small beetles that had burrowed into the pellets. Wilson (1938) found that small pellets decompose within four to six weeks during the spring, but last 3-5 months during winter. Of course, it is always difficult to find the owls themselves. Diurnal observations are also the only way to gather data on nesting behavior and success and the only way to observe the owl, although this is only during the owl's less active time.

Listening for voluntary vocalizations is a seasonal method, but at the right time of year it is more efficient in detecting Saw-whet Owls than daytime searches. It is also the only way of those methods we used to observe nocturnal behavior of the owls unaffected by human intrusion. During our listening sessions, we noted instances in which Saw-whet Owls appeared to approach and respond to each other, apparently oblivious to their human audience.

Auditory censusing at the right time of year is by far the most efficient means of censusing Saw-

whet and Eastern Screech-Owls. One must, however, determine the peak calling period of the Saw-whet Owls in the area if one wishes to census an area in the fewest evenings. For example, on 9 March, we elicited responses from all the owls we ever detected in the area we censused that night; however, we can only know that from repeated surveys of the area. We only experienced 100% detectability twice, on 9 March at Devil's Lake south shore and on 27 March at the Steinke Basin, so it probably is not a common occurrence. Tape playback and, more time intensively, listening for voluntary vocalizations enable censusing of areas that are all but inaccessible on foot. Calling data also greatly improves the efficiency of visual searching during the day.

One method we did not use is banding/recapture. This requires location of the owl on a day roost, capture of the owl, attaching a band and/or other visual markers on the owl, release, and attempts to re-identify the same individual by recapture. This is one way of monitoring the location of individual owls. We have considered this method, but feel it is not appropriate for our purposes. Mumford and Zusi (1958) found that the bands and marks they placed on Saw-whet Owls were rarely observable without recapturing the owl and they were often unable to catch a given owl to confirm its identity. Frequent recapture of the owls is likely to affect their behavior, thus biasing the results. From our observations of the diurnal behavior of the Saw-whet Owl, we believe that Saw-whet Owls become increasingly skittish the more human intrusion they experience and become more inclined to flush off their

roosts and roost in progressively more inaccessible locations the more often the intrusions occur.

Radiotelemetry is the best method of collecting data on the movements or site fidelity of an owl. It has been used to study home range size and habitat use (Forbes and Warner 1974) and roost site selection (Hayward and Garton 1984) in Saw-whet Owls. This requires capturing the owl only once, and allows the observer to monitor the owl from a distance. We have also not attempted this method.

METHODS OF ANALYZING DATA ON SAW-WHET OWLS

We analyzed the results from the three methods of detection together in order to reveal the most about the individual Saw-whet Owls. First, we marked the location and date of all records of Saw-whet Owls on an enlarged 1:24,000 topographic map. Visual records were indicated by a dot and calling records by drawing a line from our listening station in the direction of the calling station of the owl. We used the term calling station (Savage 1965) for each calling site.

However, we needed to determine the locations of the calling records more precisely than simply a point somewhere along a straight line of unknown length. We identified the instances where the calling station could be triangulated because we heard the same owl in the same evening while we were at different listening stations. We measured on the map the length of each triangulating (intersecting) line from the listening station to the point where the lines intersected. The point where the lines intersect is the approximate location of the owl.

We grouped the triangulation data according to the habitat between the calling owl and our listening station (e.g. open area or forest), since the detection distance of Saw-whet Owl calls varies according to the habitat through which it is heard (table 1). The different vocalizations of the Saw-whet Owl probably also vary in detection distance, but we believe the series (typical) call has the

Table 1. Detection distance of Saw-whet Owl songs in different habitats.

Habitat			-----Distances-----		
	N owls	N	mean (m)	range (m)	median (m)
Forest	6	18	172.5	92-280.5	150-157
Mixed Forest-	5	10	297	225-393	281-292
Open Area					
Open Field	1	3	546	472-674	494
Across Lake	2	5	1084	983-1236	1056
Brushy Area	1	4	76	45-112.5	61.5-84.5

Note: When more than two lines triangulated a particular calling station, the line did not always intersect precisely. In that case, we used the range of distances each line could be when calculating the median and the average of these distances in calculating the mean.

greatest audible distance of the calls we have heard, if only because there is generally a greater amount of time in which to hear it. Therefore, we used only the series call in the triangulation analysis. We calculated the detection distance to triangulated owls in each habitat type--forest, mixed open and forest, open areas (lake and field), and open brush, although the sample size was small for the last two categories.

We reasoned that the mean distance of triangulated calling stations from the listening station provided a statistically valid basis for estimating the location of untriangulated calling records. Thus, we marked the mean distance from listening station to calling station of triangulated records in the appropriate habitat on the lines we drew on our maps for each untriangulated calling record to indicate the probable location of the owl's calling station. If there was reason to believe that the record was appreciably closer or farther than the mean distance in that habitat, we indicated both the minimum and mean, or the mean and maximum distances as appropriate. Thus, our maps now had dots to indicate visual records and either a dot or a line segment to indicate calling records (fig. 2).

Next we determined the minimum number and location of composite calling stations (composites), a term we coined to denote all the calling stations in an area used by a single owl. The scattered distribution and considerable density of calling records precluded any obvious conclusions about how many owls we had detected. We used simultaneous or nearly simultaneous calling by nearby owls on a given night as the basis for designating different owls for two calling stations. We drew boundary lines separating these calling stations from each other (fig. 2). All stations grouped together, rather than separated from each other, by these lines belong to the same composite calling station. We drew a circle around each composite as a visual aid in our research (fig. 3 and 4). These circles are not intended to represent territories.

We used the estimated detection distance in each habitat to create a strip map of the area covered by our auditory censuses (fig. 1). The width of the strip map at each listening station depends on the openness of the habitat at that station. We drew arcs from each listening station at the estimated detection distance for the habitat to generate the margins of the strip census area.

Since a Saw-whet Owl at the maximum detection distance from the nearest listening station is not likely to be audible from another listening station it would be rare to triangulate an owl that was barely audible. For this reason we believe that our greatest triangulation distances for the owls were slightly shorter than the actual detection distance. We estimate that the detection distance of Saw-whet Owls in our area was about 300 m through forests, 400 m through mixed forest and open areas, and 700 m over open fields. These figures are all slightly higher than the greatest triangulation distances in their respective habitats that are listed in table 1 but are rounded up within the error allowance for

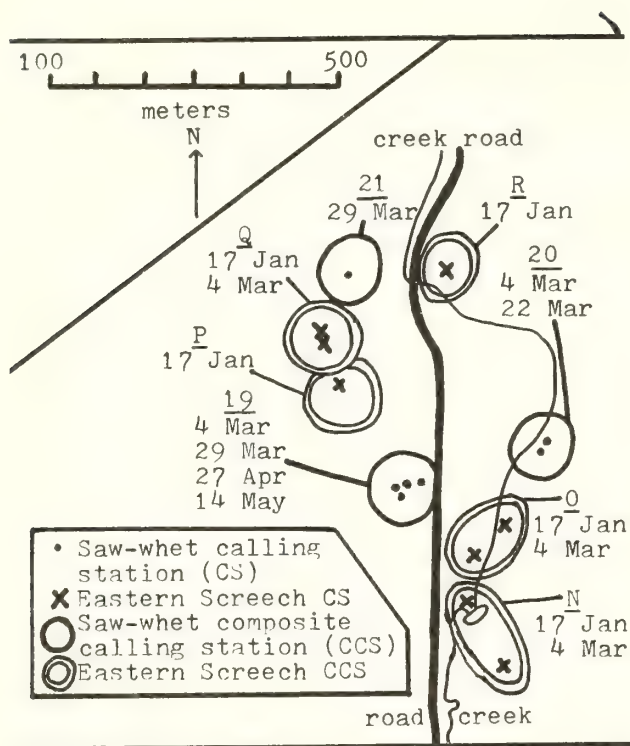


Figure 4. Map of Baxter's Hollow, indicating the calling stations and composite calling stations of Saw-whet Owls and Eastern Screech-Owls.

the scale of our map. We did not extrapolate a detection distance from the triangulations in open brushy areas; the only such area was very small and was immediately adjacent to our transect.

Since we determined the number of composite calling stations and created the strip map, we were able to calculate the density of Saw-whet Owls per unit of censused area. We also calculated the area of forest and area of open habitat in our strip census area based on the vegetation analysis in Druckenmiller (1978) and then calculated the density of Saw-whet Owls per unit area of forest, since we found Saw-whet Owls only in forested areas.

RESULTS OF ANALYZING DATA ON SAW-WHET OWLS

We identified 25 composite calling stations for Saw-whet Owls, numbered 1-25, with 18 in the Devil's Lake south shore area, 3 at Baxter's Hollow, and 4 in the Steinke Basin (fig. 3 and 4). Table 2 lists the calling time range for each composite calling station. If we eliminate from consideration those composites which received only one day of listening observation (composites 13, 16, and 17), the average calling period per composite was 28.1 days (range 1-71, median 31 and 33 days), with 3.1 calling records (range 1-7) per composite.

We believe that each composite calling station is used by only one owl for several reasons. First, although we noted five instances in which an owl moved, three occurred during our listening sessions for voluntary vocalizations. At such times we were

Table 2. Calling records per composite calling stations (CCS) of Saw-whet Owls.

CCS	Range of calling records	N	Calling range (days)	Range of listening dates	N lis- tening dates
1	9 Mar-14 Apr	2	36	9 Mar-14 Apr	2
2	9 Mar-29 Mar	2	20	9 Mar-14 Apr	3
3	9 Mar-11 Apr	2	33	9 Mar-14 Apr	3
4	9 Mar-14 Apr	3	36	9 Mar-14 Apr	3
5	9 Mar-26 Apr	2	48	9 Mar-26 Apr	5
6	9 Mar-22 Apr	4	44	9 Mar-26 Apr	7
7	9 Mar-22 Apr	6	44	9 Mar-26 Apr	8
8	21 Feb-11 Mar	6	18	21 Feb-26 Apr	14
9	24 Feb-14 Apr	2	49	24 Feb-26 Apr	13
10	19 Feb-17 Apr	7	57	19 Feb-26 Apr	15
11	24 Feb-11 Mar	4	15	21 Feb-14 Apr	10
12	1 Mar-11 Mar	3	10	24 Feb-14 Apr	8
13	11 Mar	1	1	11 Mar	1
14	1 Mar	1	1	1 Mar-13 Mar	2
15	3 Mar-13 Mar	2	10	3 Mar-28 Mar	3
16	14 Mar	1	1	14 Mar	1
17	16 Mar	1	1	16 Mar	1
18	9 Mar-14 Apr	3	36	9 Mar-14 Apr	4
19	4 Mar-14 May	4	71	4 Mar-14 May	4
20	4 Mar-22 Mar	2	18	4 Mar-14 May	4
21	29 Mar	1	1	4 Mar-14 May	3
22	16 Mar-19 Apr	5	34	16 Mar-27 Apr	6
23	27 Mar	1	1	27 Mar-27 Apr	4
24	27 Mar-27 Apr	4	31	27 Mar-27 Apr	4
25	22 Mar-27 Mar	2	5	27 Mar-27 Apr	5
19 Feb-14 May		71	1-71	19 Feb-14 May	

Notes: Other competent observers provided one record each of owls 3, 4, 19, 20, and 25; these records are included in N calling records and in N listening dates. Owls within range that they did not hear are not counted. Auditory censusing for Eastern Screech-Owls within range of a Saw-whet Owl is counted as a listening date only if the Saw-whet responded. Owl 9 was always barely within our audibility range. Audibility of owl 23 declined drastically in April because of frogs. Listening dates after the date of last calling by a Saw-whet Owl (1 May) are excluded. Listening dates on which audibility was poor are also excluded. Several owls responded to tapes being played across the lake, a distance of a kilometer. We counted such cases as listening date only when the owl responded.

sedentary and listened to each owl for a longer period of time. In these cases, if the calling owls were responding to a vocalization, they were responding to a neighboring owl instead of a recording. However, during auditory censusing, we noted many more triangulations than movements, indicating a strong tendency to remain on one perch, even when several neighbors responded at the same time to the tape. Second, many Saw-whet composites had a time range exceeding a month, indicating considerable consistency and site fidelity by the owls. The simplest explanation for this pattern is that the same owl is responsible for all the calling records in the area of each composite calling station.

Thus, we believe that the composite calling stations we have identified are each used by one owl. Furthermore, from the evidence of several of the composites--5, 19, and 22 in particular--we believe that a good number of the composites correlate with the territories of resident Saw-whet Owls, although we do not know how large the territories are. The data for many of the composites are scanty enough to permit other interpretations, such as wintering or transient owls. Most owls called for too long a period from the same area to be transients. Catling (1971) found that owls he located and banded during the spring migration near Toronto, where the latitude (43° 41' N) is similar to that of our study area, were invariably gone from the area within two days. In the absence of vocal records, it is difficult to confirm the presence of a Saw-whet Owl in late spring and beyond. As further corroboration that the species is resident, we sighted an owl in composite 22 on 1 July and two competent observers sighted an immature Saw-whet Owl on 1 June in another area of the Baraboo Hills of Sauk County (K. Lange and P. Druckenmiller, pers. comm.). We also found a few pellets regularly throughout the summer in the area of composite 22.

The detectability of Saw-whet Owls was very high in March and dropped considerably in April. Saw-whet Owls began calling voluntarily around sundown while it was still twilight and remained responsive to the tape well after that. We did not continue to listen for voluntary calling after an hour past sundown--sometimes an owl was calling as we terminated the listening session, and we did no observations of any kind after 2200 hrs. Once we heard a Saw-whet Owl call during the day (1112 hrs on 23 March) after we had done a visual search of the area. The series (typical) call is generally audible for only several hundred meters, but we have occasionally heard this call across Devil's Lake for a distance exceeding 1 km (table 1).

During the listening sessions for voluntary calling, we were nearest owl composites 8 and 10. These composites are across the road from each other. On two evenings (24 February and 4 March), these two owls called simultaneously. On the latter date, we noted much interaction between these two owls. At 1739 hrs, owl 8 initiated calling and the two exchanged vocal responses nine times until 1837 hrs. During this time, both owls moved toward each other and then away from each other. On 7 March, owls 8 and 12, also adjacent to each other, exchanged vocal responses three times. Owl 10 did not call during the listening session that evening.

The census area along our strip transects contained 3.60 km² from which Saw-whet Owls were audible. The population density was 5.0 calling Saw-whet Owls/km² and 7.2/km² of forested area. One 116-hectare area, from stops 4 to 27 and stops 57 to 60, intersecting each other, contained 15 calling Saw-whet Owls, for a maximum density of 12.9/km² and 15.8/km² of forested area. In this high density area we found calling owls at approximately 250 m intervals along the transect. Because of the even distribution of owls in this area and our numerous censuses of it, we believe this density approaches

the maximum density of the species in this habitat and area.

DISCUSSION

Catling (1971) found that the spring migration of Saw-whet Owls near Toronto began about 24 March, peaked 12-20 April, and ended about 25 April. Our results suggest that most of the Saw-whet Owls we heard were either winter residents or breeding birds. We heard five different owls call after 20 April, which is the end of the peak migration period at our latitude (Catling 1971). Catling also states that Saw-whet Owls wintering in his area left during March. Owl 22, in whose composite we saw a Saw-whet Owl on 12 May and 1 July, did not call after 19 April. For this reason, we believe that failure to hear certain owls after mid-April does not necessarily mean they had left the area. Also, our main census route receives so much usage by people from May to September that censusing is very difficult during these months. Although 18 of the 25 Saw-whet Owls that we found were along this route, our three latest calling records were from other areas, where human-generated noise was not as much of a problem. Brewster (1925) noted a calling period for Saw-whet Owls in Maine that was similar to ours, tapering in late April and becoming irregular in May.

Studies in Wisconsin (Follen 1981, 1982) and Michigan (Curtis 1963a, b) indicate that the most likely egg laying period at our latitude is early April. Follen and Haug (1981) reported a nest with eggs on 18 March about 100 km NNW of our study area. Since the incubation period for Saw-whet Owl eggs is 26-28 days and the fledging period is about 34 days (Eckert and Karalus 1974), the fledged immature Saw-whet Owl seen on 1 June 1986 in the Baraboo Hills must have hatched from an egg laid no later than the first week of April. Since nest initiation occurs around the beginning of April, many of the Saw-whet Owls we heard (12 out of 20 composites censused after 10 April) were calling during the normal breeding period and may well be breeders. Coincidentally or not, the responsiveness of Saw-whet Owls to taped calls dropped markedly during the first half of April, when most eggs are probably laid.

Our maximum density of 12.9 calling Saw-whet Owls/km² and 15.8/km² of forest is similar to the density of one pair/40 acres (12.4 individuals/km²) reported by Johnson et al. (1979) in Arizona, but we do not know whether they assumed a pair was present for each calling owl. Simpson (1972) conducted auditory censuses in North Carolina at the southern tip of the eastern breeding range of Saw-whet Owls and found one active calling station per 2.63 km of transect, a much lower density than we found. Vanderschaegen (1981) and Follen (1981) mention instances of large numbers of Saw-whet Owls occurring in two areas of northern Wisconsin, but do not give density estimates.

CENSUS OF EASTERN SCREECH-OWLS

Along the 4.4 km of census route surveyed for

Eastern Screech-Owls (*Otus asio*) with tape playback, we found 13 Screech-Owl composite calling stations, lettered A-M (fig. 3). In Baxter's Hollow, we found five, lettered N-R (fig. 4). We mapped these records according to the methods described for Saw-whet Owls. We did not have a sufficient sample of triangulations for this species to determine detection distances. However, we used the few triangulations available to assist in mapping the records accurately. Habitat features also helped, in that open areas beyond and interspersed in the forests lining the route limited the possibilities for roost locations. We noted pairs when two voices overlapped from the same location. We considered the composite for each member of the pair to overlap completely with the other's, although this may be proven wrong with further research. The number of Screech-Owls was determined in the same way as for Saw-whet Owls, by noting records from different locations on the same night.

Eastern Screech-Owls also showed a strong pattern of consistency in their composite calling stations. This is not surprising since they are a resident species. Although Screech-Owls showed more of a tendency than Saw-whet Owls to move in response to the tape, they usually stayed in one place. It is easier to determine whether a Screech-Owl has moved because of the distinctive pitch and style of individual Screech-Owl voices.

The distribution of Saw-whet Owls and Eastern Screech-Owls was remarkably disjunct, with only slight overlap of these species; this segregation was statistically significant ($P < .001$). Saw-whet Owls occurred in large tracts of forest, including pine plantations, whereas Screech-Owls occupied forests with more open areas ($P < .001$). We found neither species of owl in the area from stops 27 to 33, between the area of Saw-whet Owl concentration and the area of Eastern Screech-Owl concentration. This area is vegetated with lowland deciduous forest, a southern forest type.

We noted 11 instances of interspecific call answering to taped call by these two species during our playback census. Five individual Saw-whet Owls responded six times to Eastern Screech-Owl tapes, and three to five individual Screech-Owls responded to Saw-whet tapes. Hayward (1983) has also noted interspecific call answering by Saw-whet Owls.

VOCALIZATIONS OF SAW-WHET OWLS

We noted a variety of vocalizations for this species. The territorial song was by far the most commonly heard vocalization. It consisted of a single short high-pitched note which was repeated at consistent intervals, often for a great length of time. Volume sometimes varied, although after careful observation it generally became apparent that the owl had not moved appreciably. The owl had probably been projecting its call in several directions, and this probably accounts for the ventriloquist effect reported by some authors. If the vocalization lasted sufficiently long for us to pinpoint its direction, we did not find this "ven-

triloquism" confounding. If the owl moved between vocalizations, great care was required in attributing the vocalization to the right individual. As discussed above, we noted several times in which movement by an individual owl was apparent. We do not believe that the owls were moving about very much because of the consistency of each composite's location. Sometimes an owl accelerated the rate of the notes in the song. Conversely, we have also noted an interval greater than the observed norm. The series vocalization is well known and is represented on various bird song recordings, such as "Voices of New World Nightbirds" and "A Field Guide to Bird Songs of Eastern and Central North America" mentioned above.

We also identified four additional vocalizations: a harsh, short shriek (probably an alarm call); an ascending, single-noted wail ("saw-whet call"), a single, long whistle similar in pitch and tone to the song note, and a lower-pitched, isolated descending call. We attributed these vocalizations to the Saw-whet Owl on the basis of one or both of the following means. First, the vocalization immediately preceded or followed the song and came from the same direction and at comparable volume. Second, the location of the vocalization triangulated with a record of a series call on the same evening. The "saw-whet" call is also on "A Field Guide to Bird Songs of Eastern and Central North America."

ROOSTS OF SAW-WHET OWLS

We found Saw-whet Owl roosts in seven species of coniferous trees in our study area: White Spruce (*Picea glauca*), Jack Pine (*Pinus banksiana*), Red Pine (*Pinus resinosa*), Eastern Red Cedar (*Juniperus virginiana*), Eastern White Pine (*Pinus strobus*), Eastern Hemlock (*Tsuga canadensis*), and Norway Spruce (*Picea abies*). Over 95% of the roosts were in five species of trees--White Spruce, Jack Pine, Red Pine, Eastern Red Cedar, and Norway Spruce. The roost height was positively correlated with the height of the tree and was low in densely foliated trees and high in sparse trees. Table 3 shows that the mean roost height and mean tree height is lowest for Eastern Red Cedars, the densest of the five trees, followed in order by Jack Pine, White Spruce, Norway Spruce, and Red Pine.

Although we found many pellets under Red Pine, we were usually unable to determine how high the owl had roosted, since there were few branches to catch

Table 3. Typical roost sites of Saw-whet Owls.

-----Tree-----			-----Roost-----		
species	mean height (m)	N	mean height (m)	sd (m)	range (m)
Eastern Red Cedar	4.3	5	1.57	0.32	1.37-2.13
Jack Pine	5.3	33	1.91	0.64	0.76-3.66
White Spruce	6.6	41	2.76	0.79	0.69-4.88
Norway Spruce	10.1	5	4.38	2.09	1.95-7.30
Red Pine	11.6	6	5.92	1.32	3.96-7.62

white wash below the roost to give us clues where the exact roost site was. Saw-whet Owl roosts in Red Pines were usually about 6 m high, just above where the foliage begins, and averaged 63 cm (N=7) from the trunk; below these roosts most of the limbs were broken stubs with no needles, as is typical in Red Pine plantations. A well hidden Saw-whet Owl is nearly impossible to spot when it is high in a Red Pine. Furthermore, in the summer the evidence of a roost--wash and pellets--on or near the ground is erased rapidly by weather and insects, which makes it more difficult to identify a roost tree. For these reasons we believe that Saw-whet Owls probably roost in such tall trees more often than is indicated by the frequency with which they are found there. Hayward and Garton (1984) used radiotelemetry to locate Saw-whet Owl roosts and found Saw-whet Owls roosting as high as 7.3 m, with a mean height of 4.2 m (N=15). It took up to 45 minutes to find the owl after they had located the roosting tree, indicating how difficult Saw-whet Owls are to find when they choose high roosts.

At Mirror Lake Pine Barren Saw-whet Owls frequently roosted in dense 3-6 m tall Eastern Red Cedars that were scattered widely and singly across the open dry prairie or on the edges of Jack Pine clumps. Only the largest Red Cedars were chosen. Roosts tended to be less than 2 m high--at or lower than the widest point of the tree. The roost location ranged from near the trunk to near the tips of the branches, but was usually in the outer part of the foliage (mean=107 cm from the trunk, N=9).

Roosts in Jack Pines were in trees of all sizes, but most were in small trees in dense clumps. Some roosts were in large sprawling Jack Pines that had many limbs intersecting one another 1-4 m off the ground. Roost locations ranged from near the trunk to 2/3 of the way out on the branch, with the mean 53.2 cm from the trunk (N=36).

White Spruce roosts were generally 2-4 m high and close to the trunk of the tree (mean=27.4 cm, N=38). In general, these trees afford considerable cover from all directions and the plantations or dense forests are difficult to traverse. One plantation yielded pellets throughout the year and produced our only summer sighting of a Saw-whet Owl on 1 July. Many winter roosts were along a hiking-skiing trail that bisects the plantation. During the late spring and summer the owl seemed to choose more secluded roosts in the interior of the plantation. This may have resulted from our frequent visits to the area to collect pellets.

Roosts in Norway Spruces were all in fairly tall trees and were intermediate in height between White Spruces and Red Pines. The two highest roosts in Norway Spruces were in a tree at the edge of a plantation. Roosts tended to be close to the trunk in this species (mean=18 cm, N=4).

PELLET ANALYSIS

We collected 431 Saw-whet Owl pellets between 17 March and 17 December. Saw-whet Owl pellets are

very compact and are usually dark and moist when fresh. Typical pellets were 2.5-4.0 cm long and 1.3-1.7 cm wide (mean length= 3.05 cm, range=1.8-5.1 cm, N=344 unbroken pellets; mean width=1.54 cm, range=0.9-2.0 cm, N=396 pellets).

We analyzed 380 pellets, using Driver (1949), Jackson (1961), Glass (1973), and Burt and Grossenheider (1976) to identify the mammal skulls. Table 4 lists the prey items found in the pellets. There were 0.64 prey items per pellet, which agrees with the findings of Collins (1963) and Errington (1932) that Saw-whet Owls frequently cast two pellets per prey item eaten. Over 90% of prey individuals were rodents, and over 80% of the prey items were Peromyscus. Peromyscus has been the dominant prey in most studies of Saw-whet Owl diets, e.g. Errington (1932) and Graber (1962), in the midwest United States. Microtus was the second most important prey item. We also found a few Sorex and Blarina shrews, one Myotis bat, several small birds, and one cricket in the pellets. Terrill (1931) also found Myotis in the diet of Saw-whet Owls.

The Saw-whet Owl prey was heavily slanted toward woodland species. Over 90% of the Peromyscus identified were P. leucopus, a forest species; the rest were P. maniculatus, a field species. Microtus is an open country genus in our area, while Sorex cinereus is generally a forest species. Blarina brevicauda is ubiquitous, and Myotis likewise could be found almost anywhere. Excluding the one rodent, birds, and cricket, whose prime habitats are unknown since we couldn't identify them to species, about 188 prey individuals were forest-dwelling species, 37 were open-country species, and seven were widely

Table 4. Prey items found in 380 Saw-whet Owl pellets collected 17 March to 17 December

Prey Item	N individuals (%)
Mammals (95.9%)	
Rodents (90.9%)	
<u>Peromyscus</u> spp.	195 (80.2)
<u>P. leucopus</u>	121
<u>P. maniculatus</u>	8
unidentified <u>P.</u>	66
<u>Microtus</u> spp.	25 (10.3)
<u>M. pennsylvanicus</u>	17
<u>M. ochrogaster</u>	2
unidentified <u>M.</u>	6
unidentified rodent	1 (0.4)
Shrews (4.5%)	
<u>Blarina brevicauda</u>	6 (2.5)
<u>Sorex cinereus</u>	5 (2.1)
Bats (0.4%)	
<u>Myotis</u> spp.	1 (0.4)
Birds (3.7%)	
Finch spp.	2 (0.8)
unidentified Passerine	7 (2.9)
Insects (0.4%)	
cricket	1 (0.4)
Total	243 (100.0)

adapted species. Therefore, over 80% of the prey was gleaned from the forest floor. Saw-whet Owls that lived in more open Red Pine plantations or that roosted in Eastern Red Cedars in open parts of Mirror Lake Pine Barren took proportionately more open-country prey than their counterparts in denser White Spruce or Jack Pine stands. These Saw-whet Owls living in more open habitat took 40% Microtus and 51% Peromyscus versus the 5% Microtus and 85% Peromyscus for the Saw-whet Owls living in denser forests in the same region.

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Remigial Molt in Fall Migrant Long-Eared and Northern Saw-Whet Owls¹

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Abstract.--Netting operations at the Hawk Ridge Nature Reserve, Duluth, Minnesota resulted in the capture of 1,090 Long-eared Owls from 1976-86 and 2,639 Northern Saw-whet Owls from 1980-86. Adults and juveniles can be separated by the presence or absence of (1) 2 generations of remiges and/or (2) sequentially grown remiges, which are characterized by a pink color on the undersurface that fades with time. The proportion of adult Long-eared Owls with completed remigial molt varied from year to year, ostensibly in relation to prey abundance. In contrast, virtually all adult Saw-whet Owls had retained remiges from the previous year, with 3 basic molt patterns that appeared to correspond with different age classes.

INTRODUCTION

Patterns of molt provide a basis for ageing many species of birds for banding (Anonymous 1977). Previous studies on the molt patterns of Long-eared Owls (*Asio otus*) mainly have been concerned with captive birds (Haarhaus 1983, Wijnandts 1984) and a few individuals encountered in the wild at various times of year (Stresemann and Stresemann 1966). We are not aware of published data on molt patterns of remiges in Northern Saw-Whet Owls (*Aegolius acadicus*). Mueller and Berger (1967) aged adult Saw-whet Owls by the presence of 2 generations of remiges, but at that time it was not known whether they resulted from an interrupted molt or an incomplete annual molt (J. Sheppard, Bird Banding Lab., pers. comm.). Subsequent studies also have relied on the presence of 2 generations of remiges in ageing saw-whets (Evans 1975, Sheppard and Klimkiewicz 1976, Anonymous 1977, Weir et al. 1980, Buckholtz et al. 1984). Weir et al. (1980) suggested that the 2 generations arise from an interrupted molt, while Buckholtz et al. (1984) attributed it to a

partial postbreeding remex molt. In this paper we present molt patterns in fall migrant Long-eared Owls captured from 1976 to 1986 and in Saw-whet Owls captured from 1980 to 1986. We also discuss the patterns' relationship to ageing owls and ecological factors that may influence observed patterns.

METHODS

Trapping by mist net ('CTX', Northeastern Bird-Banding Assoc.) was conducted nightly from mid September to mid November at the Hawk Ridge Research Station, Hawk Ridge Nature Reserve, Duluth, Minnesota. The study area, net placement, and owl capture techniques are described in Evans (1980).

In addition to banding and taking weight, wing, and tail measurements, we recorded the molt of right wing remiges and rectrices for all adult owls. Long-eared Owls could not be reliably sexed, although we did assign sex based on underwing coloration -- males being paler and less buffy than females. We also had difficulty sexing Saw-whet Owls. Measurement criteria presented by Sheppard and Klimkiewicz (1976) and Buckholtz et al. (1984), when applied to our captures, resulted in a sex ratio heavily skewed toward males and we have little confidence in the applicability of those criteria to the Saw-whet population migrating through Duluth. Beginning in 1977, we applied permanent green dye (Sanford's Marker) to remiges of all Saw-whet Owls to evaluate the age

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status of retained feathers in birds recaptured in subsequent years.

RESULTS AND DISCUSSION

Long-eared Owls

We captured 1,090 Long-eared Owls, of which 394 (36.1%) were adults (table 1). The yearly juvenile/adult ratio ranged from 0.5 to 4.3, with an overall ratio of 1.8. Of the adult owls, 194 (49.2%) had completed their molt and had only 1 generation of remiges; these were aged by the presence of pink color on the undersurface of the remiges. This pink wash is most apparent on newly grown feathers and fades over a period of several months. Since adult primaries grow sequentially from P1 to P10 (Wijnandts 1984) the pink wash increases in intensity toward P10, in contrast to juveniles, in which the pink wash is well faded and uniformly colored. There usually is marked contrast in pink wash between S4 and S5 (the molt center), which is often helpful in ageing some birds (probably females) whose buffier underwing color tends to obscure the pink wash in the primaries. Of the adult owls, 200 (50.8%) still retained old feathers from the previous year (the molt column in table 1 totals 197 because molt records were lost for 3 owls, 1 each in 1978, 1981, and 1984). Table 2 presents the total number of old feathers at each remex position for owls with molt (no owls had old rectrices). Adult owls with retained old feathers had a mean of 0.1 old

primaries and 4.1 old secondaries. Rounding these averages off to the nearest whole feather and applying them to the highest frequencies in table 2 to identify locations, we derived a 'generalized composite' of a typical adult long-ear with incomplete molt (fig. 1). Wijnandts (1984) found that primary molt proceeded descendently from P1 and secondary molt proceeded descendently from molt centers at S1 and S5 and ascendently and descendently from a third molt center at S11. Thus, the last secondaries to be molted typically were S4, S7, and S8. In general, our observations are in agreement; however, we observed a number of birds that had begun molt at S2 or S3, retaining old feathers only at S1 (6) or S1-2 (9). Eliminating these birds from the frequencies in table 2 resulted in a 'generalized composite' that more accurately reflects the typical owl with retained feathers observed at Duluth in the autumn (fig. 2). The frequencies of old feathers at the molt foci (S1, 5, and 11, table 2) suggest that molt is more likely to be initiated at S5 and 11 than at S1, perhaps reflecting stronger hormonal influence. Indeed, it was not uncommon for the molt center at S1 to remain inactive,

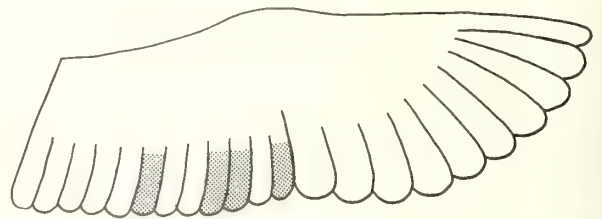


Figure 1.--Original generalized composite derived for a typical adult Long-eared Owl with molt (old feathers shaded).

Table 1.--Yearly numbers of Long-eared Owls captured at Duluth, Minnesota, 1976 - 1980, and number of adults with molt.

Year	Juvenile	Adult	Molt	%
1976	95	42	19	45
1977	49	26	17	65
1978	111	60	56	93
1979	56	23	18	78
1980	96	37	11	30
1981	88	71	22	31
1982	30	61	20	33
1983	17	13	11	85
1984	56	13	5	38
1985	26	8	2	25
1986	72	40	16	40
Total	696	394	197	50

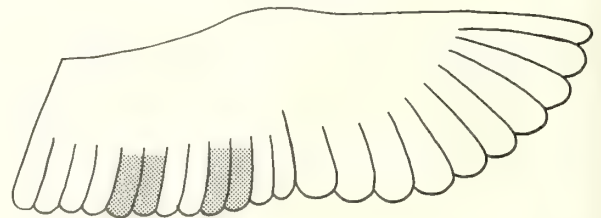


Figure 2.--Revised generalized composite derived for a typical adult Long-eared Owl with molt (old feathers shaded).

Table 2.--Total number of old feathers at each feather position in the right primary (RP) and right secondary (RS) of 197 adult Long-eared Owls with molt.

RP	1	1	1	1					1	3	5		
	1	2	3	4	5	6	7	8	9	10	11	12	
RS	106	103	108	133	38	72	112	96	4	0	7	0	0

resulting in an otherwise cleanly molted bird with old feathers at S1-4.

Almost all Long-eared Owls had completed primary molt. Only .5 of the 197 owls with retained feathers had not finished molting their primaries. Three of these birds occurred in 1978, which had the highest yearly proportion of owls with molt. One apparently aberrant individual had only replaced P5-7, had S1-10 old, and had all 12 rectrices just emerging from sheath. The remaining 4 had a pattern consistent with descendent primary molt, with P9-10 old (table 2). Of the owls with retained feathers, 84 (42.6%) also had actively growing feathers. These included a total of 107 primaries (predominantly P9-10) and 68 secondaries, which were invariably in a sequence consistent with the molting pattern described by Wijnandts (1984) and observed in this study. The mean length of growing feathers (recorded in tenths) was 8.2 for primaries and 8.0 for secondaries; only 12 of 107 primaries and 5 of 68 secondaries were less than 7/10 grown. Thus it appears, for the most part, that active molting ceases with the onset of migration. We captured only one owl that had two generations of old feathers. We conclude that the old, retained feathers observed in fall migrant long-ears are the result of an interrupted molt, which is completed sometime after migration.

The proportion of adult long-ears that had not completed their molt varied considerably among years, from a high of 93% to a low of 25% (table 1). We feel that prey availability during the molting period may explain the variation observed. With peaks in 1978 and 1983 and lows in 1980 and 1985, the proportion of incompletely molted owls appears to vary in a regular fashion, perhaps in association with fluctuations in microtine prey. However, we found no correlation between the proportion of owls with retained feathers and the mean yearly capture weight of juveniles, adults, completely molted adults, or incompletely molted adults, although it did approach significance for adults ($r = -0.56$, 9 d.f., $P > 0.05$) and for incompletely molted adults ($r = -0.56$, 9 d.f., $P > 0.05$). With the caveat that relatively minor changes in the male/female ratio could have a substantial effect on the yearly mean capture weight, there appears to be no substantial relationship between the proportion of incompletely molted owls and capture weight. In 6 of the 11 years, mean capture weight of cleanly molted owls was less than that of incompletely molted owls, although overall it was slightly higher. To what extent the sex ratio affected mean capture weight is unknown and precludes further analysis on the relationship between the proportion of cleanly molted owls and food supply.

Saw-whet Owls

We captured 2,639 Saw-whet Owls, of which 1,463 (55.4%) were adults (table 3). The yearly juvenile/adult ratio ranged from 0.5 to 1.5, with an overall ratio of 0.8. Only 8 adults (0.5%) had completed their molt and had one generation of remiges (group E, table 3). As in the Long-eared Owls, these were aged by the pink wash on the undersurface of newly replaced remiges, which was most apparent on the outer primaries (P8-10) and at various locations in the secondaries, depending on the molt pattern involved. Care was taken in this category not to include juveniles, which often exhibit the pink wash uniformly across their greater underwing coverts as a result of their recent postjuvinal body molt. The remaining 1,455 adults had 2, and sometimes 3, generations of feathers. Considering only the 2 most recent generations of feathers, we used the molt records of individual owls to delineate 3 basic groups. A 4th group consisted of birds that could not be assigned to the above groups. In practice, placement of an owl into 1 of the 3 basic groups occasionally involved some judgement, particularly in regard to the presence of 1 and sometimes 2 'atypical' (i.e., new instead of old) feathers in an otherwise clearly apparent pattern.

Group A was by far the largest with 827 (56.5%) owls and had a pattern consisting of a solid block of old inner primaries and secondaries. Table 4 presents the total number of old feathers at each remex position for group A. Adult owls in group A had a mean of 4.2 old primaries and 3.9 old secondaries. Rounding these averages off to the nearest whole feather and applying them to the highest frequencies in table 4, we derived a generalized composite of a typical saw-whet in group A (fig. 3). This composite, with P1-4 and S1-4 old, was the most common configuration in group A (table 5).

Group B was the smallest of the 3 groups with 202 (13.8%) owls and had a

Table 3.--Yearly numbers of Saw-whet Owls captured at Duluth, Minnesota, 1980 - 1986, and number of adults in each molt pattern group.

Year	Juvenile	Adult					Total
		A	B	C	D	E	
1980	187	76	9	33	2	1	308
1981	158	165	33	45	5	3	409
1982	145	117	19	64	1	3	349
1983	61	65	29	23	3	0	181
1984	336	190	70	143	6	0	745
1985	140	106	19	51	4	0	320
1986	149	108	23	40	6	1	327
Total	1176	827	202	399	27	8	2639

Table 4.--Total number of old feathers at each feather position in the right primary (RP) and right secondary (RS) of adult Saw-whet Owls in group A, B, and C.

A	RP	826	820	777	616	357	83	14						
		1	2	3	4	5	6	7	8	9	10	11	12	
	RS	812	699	641	571	428	274	194	102	45	7	1		
B	RP	4	24	59	114	115	81	54	38	18	9			
		1	2	3	4	5	6	7	8	9	10	11	12	
	RS	38	88	104	102	122	126	120	96	57	29	12	5	
C	RP	304	259	151	132	151	189	172	103	51	25			
		1	2	3	4	5	6	7	8	9	10	11	12	
	RS	201	152	152	156	152	192	205	205	177	104	40	30	

pattern consisting of a solid block of old feathers in the mid primaries and another solid block of old feathers in the mid secondaries (table 4). Owls in group B had a mean of 2.6 old primaries and 4.4 old secondaries. Rounding these averages off to the nearest whole feather and applying them to the highest frequencies in table 4, we arrived at a generalized composite of a typical saw-whet in group B (fig. 4). There was considerable variation in the location of the respective primary and secondary blocks as can be inferred from table 4 but the respective sites were invariably consistent between primaries and secondaries (i.e., old blocks nearer the inner primaries corresponded with old blocks nearer the inner secondaries). Owing to this variation in location of old blocks there was a slight anomaly in total number of feathers between S3 and S4 in terms of portraying a solid block of secondaries. Our composite (fig. 4) includes only S4, although the actual mean of old secondaries (4.4) shows that a composite would also include S3 in about 40% of the owls.

Group C, with 399 (27.3%) owls, exhibited the widest variation in its basic pattern. It is characterized by 2, and sometimes 3, discrete blocks of old feathers in both primaries and secondaries. One block is invariably centered on the inner primaries and secondaries (similar to group A) but the position of the remaining

Table 5.--Frequency of adult Saw-whet Owls at each right primary/secondary combination of retained old feathers in Group A.

	RP	0	1	2	3	4	5	6	7	8
RS	0		3	10	2					
	1		2	17	73	11				
	2			4	26	26	2			
	3	1	1		19	44	4	1		
	4			2	25	78	37	1		
	5				7	61	76	8	2	
	6				2	21	45	11	1	
	7				4	8	66	14		
	8					8	27	18	4	
	9				3	2	12	15	4	2
	10						3	2	1	
	11							1		
	12									

block(s) was variable, as evidenced by the frequencies of total old feathers at each feather position (table 4). Owls in group C had a mean of 3.9 old primaries and 4.4 old secondaries; rounding to the nearest whole feather and applying to the frequencies in table 4, we derived the generalized composite shown in fig. 5. As in group B, the discrete blocks of old feathers were generally in comparable positions in the primaries and secondaries (i.e., a block centered at P7 had a corresponding secondary block centered at S7).

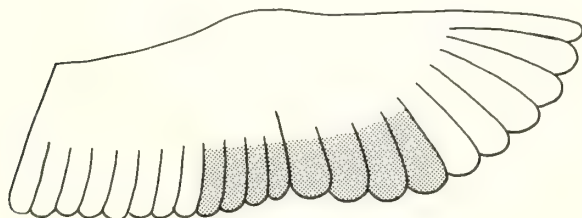


Figure 3.--Generalized composite derived for a typical adult Saw-whet Owl with type A molt (old feathers shaded).

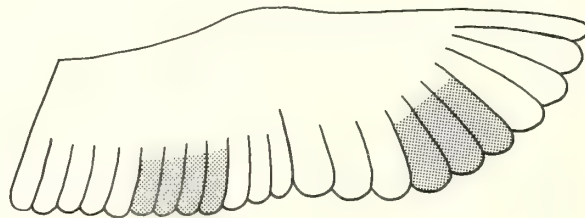


Figure 4.-- Generalized composite derived for a typical adult Saw-whet Owl with type B molt (old feathers shaded).

Group D, consisting of 27 (1.8%) owls, was composed of birds with virtually all old or all new feathers (owls with only one or two old feathers at P1 or S1 were included in group A).

As in the Long-eared Owls, some Saw-whet Owls had actively growing feathers when captured. Of the adults, 117 (8.0%) had growing feathers. These birds were evenly distributed among all groups. Growing feathers included a total of 158 primaries and 55 secondaries. Actively growing primaries invariably involved P9-10. The mean length of growing feathers (recorded in tenths) was 8.8 for primaries and 8.3 for secondaries, indicating a cessation of feather replacement with the onset of migration.

Some saw-whets had 3 generations of feathers as a result of some feathers being retained through 2 molt cycles (3 years). These occurred only in groups B, with 47 (23.3%) owls, and C, with 16 (4.0%) owls. In group B owls, the very old feathers were always found at the inner primaries and secondaries, in conformance with the Group A pattern. In group C owls, 8 had very old feathers conforming to the group A pattern and the remaining 8 showed no evident pattern.

The significance of the 3 major molt patterns was elucidated by the recapture of color marked saw-whets in subsequent years. All 4 saw-whets banded as juveniles and recaptured a year later exhibited the group A pattern and we believe that most, if not all, yearling saw-whets undergoing their first remigial molt become type A. We had no recaptures of owls known to be 2 years old but suspect that they may represent the group B pattern. Given the strong tendency for annual replacement of inner secondaries and outer primaries (see table 4), the concurrent replacement of the old group A feathers would result in a type B pattern. The relatively large proportion of group B owls retaining very old feathers, all of which were in the type A pattern, would lend support to the association between 2-year-olds and the type B pattern. Alternatively, the type B pattern may merely be a variation of the type C pattern (see below). We believe the type C pattern

represents owls ≥ 3 years old. Four of 8 owls known to be at least 3 years old did exhibit the type C pattern. However, not all owls at least 3 years old exhibited the type C pattern. Of the remaining 4 owls, 2 had a type A pattern, 1 was type B, and the 4th had only 1 old feather, or type D. Hypothetically, if we were to take the type C pattern (fig. 5) and eliminate (replace by molt) one of the two discrete (associated primary/secondary) blocks, we would derive a type A pattern by eliminating the outer block. If the inner primary/secondary block were eliminated, a type B pattern would result. At present we can confirm the existence of type A and B in owls at least 3 years old, but whether they are initially derived from a type C pattern is unknown.

The recapture of color marked saw-whets also provided some information on the progression of molt patterns from year to year. As mentioned above, the 4 owls originally captured as juveniles exhibited the type A pattern when retrapped 1 year later. One additional owl was recaptured a year later. It initially had a type C pattern and again was type C a year later, but had replaced the previous year's old feathers and retained the previous year's new feathers, so aside from the annual replacement of outer primaries and inner secondaries, it exhibited a perfect reversal of old and new feathers in the second year (figure 6). Six owls were recaptured 2 years after initial capture but not the intervening year; 2 owls exhibited a pattern progression of A-?-A, and the remaining 4 owls exhibited A-?-C, A-?-D, B-?-B, and C-?-C. We had 2 recoveries of owls 6 years later. One, originally captured as a juvenile, had a type C pattern. The other had similar type C patterns at both encounters.

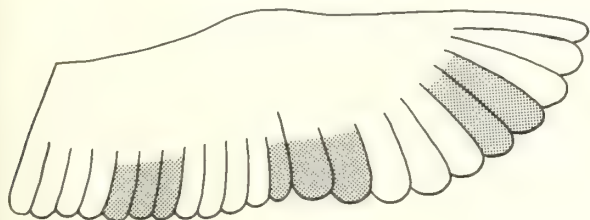


Figure 5.--Generalized composite derived for a typical adult Saw-whet Owl with type C molt (old feathers shaded).

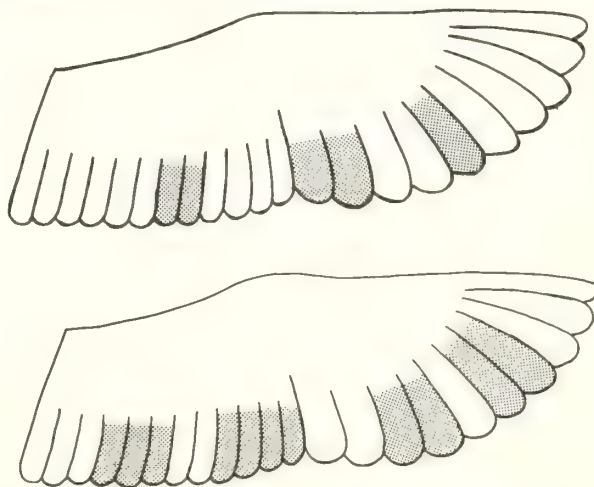


Figure 6.--Molt in an adult Saw-whet Owl captured in 1980 (top) and in 1981 (bottom) with type C patterns (old feathers shaded).

The wide variability in the 3 basic molt patterns (table 4) suggests that, as a species, the Saw-whet Owl does not exhibit molt foci in consistent locations, as is generally true in other avian species. As individuals, owls do show a tendency to retain molt foci at specific locations even though some foci are activated only in alternate years. Molt foci associated with replacement of outer primaries and inner secondaries (as well as rectrices) are activated every year. Of the 6 owls recaptured 2 years later, 2 had identical molts (A-A), one was virtually identical (B-B, with retained very old feathers at P1), and one (C-C) was roughly similar. The molt patterns of the 6 year recovery were also very similar.

Saw-whet Owls in this study retained, on average, about 35% of their remiges for 2 years. Replacement of the outer primaries, inner secondaries, and rectrices typically occurs each year. These feather tracts are in areas exposed to greater wear and abrasion than remiges in the middle of the wing. Primary feather molt in Boreal Owls (*A. funereus*) appears similar (Glutz and Bauer 1980), although retention of very old inner primaries appears to be common in 3-year-old birds and annual replacement of outer primaries is perhaps less frequent. Of 6 Boreal Owls captured during this study, 3 were type A, 2 were type C (with outer primaries and/or secondaries not replaced), and 1 did not fit our classification. The genus *Aegolius* appears unique, considering body size, in that virtually all birds have an incomplete annual molt. The retention of remiges may represent a savings in energy expenditure that is better utilized elsewhere, such as reproductive output.

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Dispersal and Mortality of Juvenile Eagle Owls Released from Captivity in Southeast Norway as Revealed by Radio Telemetry¹

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and Ole H. Stensrud²

Abstract.--Of 9 captive juvenile Eagle Owls released and radio tracked autumn 1986, 7 died within 3 months after being released; 4 due to electrocution by power lines, 1 due to wing injury, 1 due to hunting, and 1 due to starvation. The 7 birds that died had dispersed from 1.2-9.9 km, while the two that were still alive by mid-January 1987 had dispersed 33 km and 62 km.

INTRODUCTION

The breeding population of Eagle Owl *Bubo bubo* in southeast Norway has declined seriously since about 1950, and by 1975 was almost vanished in the lowlands (Fremming 1987). In order to restore this population a total of 325 juvenile Eagle Owls hatched in captivity have been released in southeast Norway each autumn since 1978. From ringing recoveries of dead specimen some knowledge has been gained about the dispersal distance, mortality rate, and mortality causes of these Eagle Owls. However, nothing is known about their habitat selection, home range size, and prey selection. Therefore, habitat management as part of the effort to restore the Eagle Owl population has so far been impossible to conduct.

Telemetry has been employed to reveal the secret behavior of nocturnal owls for more than two decades (Nicholls and Warner 1972, Forbes and Warner 1974). It has mostly been used to study habitat selection and home range size (e.g. Nicholls and Warner 1972, Forbes and Warner 1974, Bondrup-Nielsen 1978, Hayward and Garton 1984, Smith and Gilbert 1984), and more rarely to study nocturnal hunting behavior (Nilsson 1978, Wijnandts 1984, Sonerud et al. 1986). Studies on juvenile dispersal in owls by use of telemetry are few. However, one such study was conducted on Eagle Owls in Sweden (Arnkqvist et al. 1984), but comprised only 3 birds with very few data on each. In order to obtain more detailed informat-

ion on dispersal and mortality than obtained by ringing recoveries, and to obtain general information on home range size and selection of habitat and prey, we initiated a two-year study on radio-equipped juvenile Eagle Owls released from captivity. Here we report preliminary results on dispersal, mortality, and habitat selection from the first year of the study.

STUDY AREA AND METHODS

The Eagle Owls were released from Blokkemyr Eagle Owl farm in Østfold County, southeast Norway (59°11'N, 11°34'E). The study area has so far spread into Østfold and Akershus counties in southeast Norway and Göteborg & Bohus county in southwest Sweden. It is situated in the boreo-nemorale zone (sensu Nordiska Ministerrådet 1984), is fairly flat with elevations from 0-350 m, and consists of farmland interspersed with mixed coniferous-broadleaf forest.

Ten juveniles (5 females and 5 males) were equipped with a 40 g radio-transmitter (Biotrack, England) attached as a backpack, and released between September 5 - October 12 1986 (fig. 1). The birds were primarily localized from ground by cross-triangulation using a portable receiver (Televilt, Sweden) and a hand-held 4-element yagi-antennae. Cross-triangulation during daytime proceeded until the bird was sighted. The habitat it was perched in, as well as any prey or remnants thereof, were determined. If the bird was flushed, the base of its perch was checked for pellets. Nocturnal locations were determined by radio bearings alone, and the corresponding habitat determined from a map. When a bird was impossible to localize from ground, tracking was performed from aircraft. In this way, two out of three birds initially lost by ground tracking were found. All positions of localized birds were plotted on maps with scale 1:50,000. In addition, positions of localized birds within 4

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Figure 1.--Eagle Owl M3 at roost near the release site. Photography by R.S. Larsen.

km of the release site were plotted on maps with scale 1:10,000.

RESULTS

Dispersal and mortality

During the first week after release, the Eagle Owls moved around within 4 km of the release site. Between 6-9 days after release four of them died due to electrocution by power lines 1.2 to 1.6 km from the release site (table 1). Another was found with a serious wing injury, probably due to contact with power lines, 2.8 km from the release site, and was killed (table 1). The other five left this area 7-13 days after release. Two dispersed more than 10 km. These two travelled fast for about two weeks after release (fig. 2), and then settled 5-6 weeks after release (figs. 2 and 3). Of the three remaining birds, one was found alive but starving 9.9 km from the release site 16 days after release. It was kept in an aviary at the release site and fed for a week before being released again. It then stayed around the release site for six weeks,

Table 1.--Date of release and recovery, mortality factor, distance dispersed, and status per January 15 1987 for 10 juvenile Eagle Owls (F=female, M=male) released with radio-transmitters in southeast Norway during autumn 1986.

Owl	Date of		Mortality factor	Distance Dispersed (km)
	Release	Recovery		
F1	Sept. 5	Sept. 13	Electrocution	1.5
M1	" 5	" 14	"	1.3
F2	" 5	" 21		19.9
"	" 28	Nov. 23	Hunting	3.9
M2	" 21	Sept. 28	Electrocution	1.2
M3	" 21	Oct. 4	Wing injury	2.8
M4	" 21	-		28.0
F3	" 21	Oct. 27		333
"	Nov. 15	-		33
F4	Sept. 28	Jan. 10	Starvation	46.5
M5	Oct. 5	-		62
F5	" 12	Oct. 18	Electrocution	1.6

¹ Captured in poor condition and kept in aviary with unlimited food availability before new release at the original release site.

² Radio contact lost after October 1.

³ Captured with an eye injury and kept in aviary with medical care before new release at the capture site.

⁴ Died between November 16 and December 22.

taking food (dead chickens) at the aviary, until being killed, probably by humans, 3.9 km from the release site. Another bird settled in an area 5-8 km from the release site, and died due to starvation between 7-12 weeks after release. The last bird was lost after 10 days when it had dispersed at least 8 km from the release site (table 1).

For the 9 Eagle Owls that we managed to follow, dispersal distance varied from 1.2-62 km, with an average of 13 km and a median of 2.8 km (table 1). Dispersal distance did not differ between the sexes (table 1; $U=15$, $p>0.2$, Wilcoxon two-sample test, two-tailed (Sokal and Rohlf 1969)). All the 5 birds that dispersed longer than the median distance moved out in the 135° sector between southwest and north (fig. 3).

Of the 9 Eagle Owls that we managed to follow, seven died within 12 weeks after the release (78%). Of these, four (57%) were killed by electrocution, one due to wing injury, one by humans and one by starvation. The four electrocuted ones were all found within 3 m from power poles, and so were probably killed while entering or leaving a power pole, using it as a hunting perch. There was no difference in longevity between the sexes (table 1; $U=19.5$, $p>0.2$, Wilcoxon two-sample test, two-tailed).

Habitat and prey.

For the 2 Eagle Owls that dispersed longer than 10 km, we compared the habitat used with

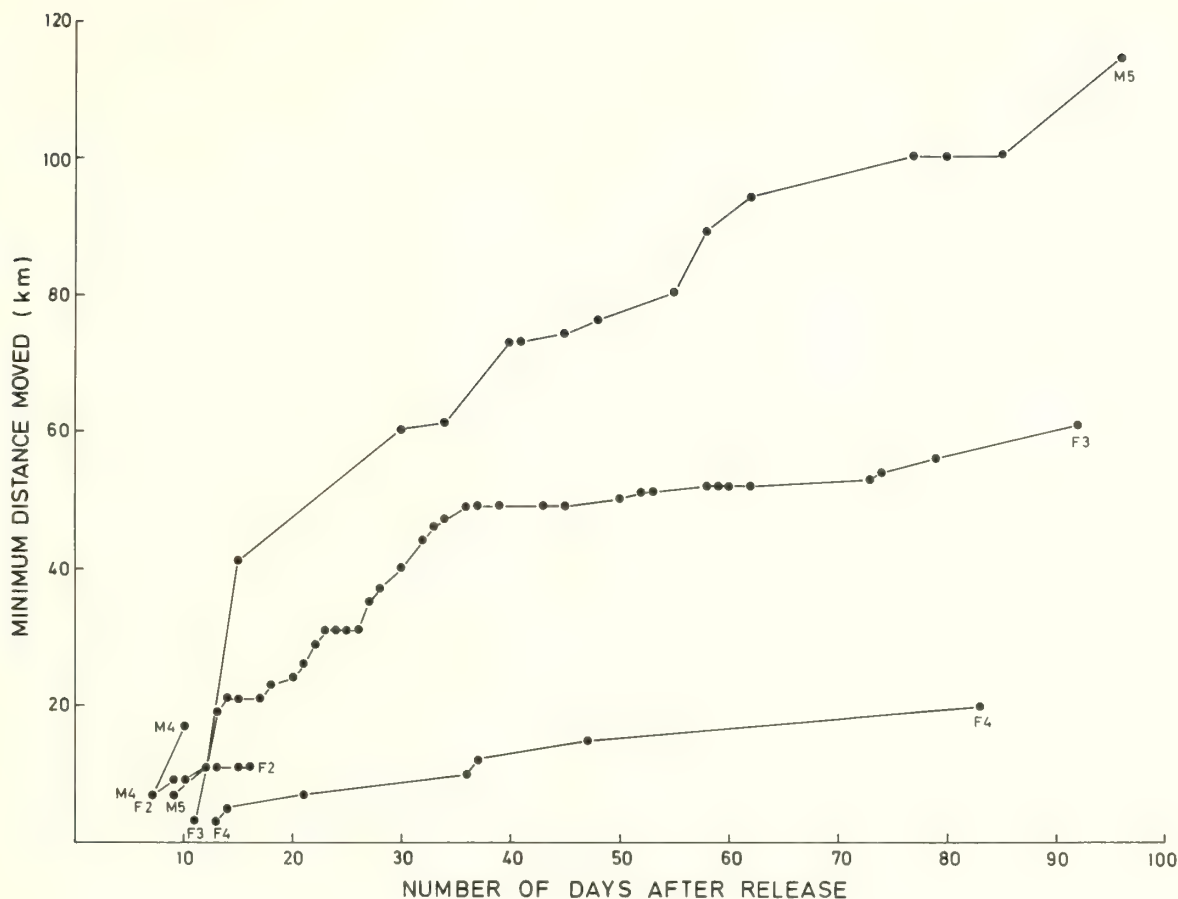


Figure 2.--Minimum distance moved in relation to time since release for the five radio-equipped juvenile Eagle Owls that dispersed farther than the median dispersal distance for all ten individuals. For more information see table 1.

that available. Both owls almost always perched in a tree or on the ground under one. The 30 relocalizations of F3 were more often situated within 200 m off water, i.e. lakes or sea, than expected by random movement ($\chi^2=18.83$, $p<0.001$), less often than expected within 200 m off cultivated fields or farmland ($\chi^2=4.97$, $p<0.05$), and as often as expected within 200 m off farm buildings, houses or cottages ($\chi^2=2.33$, $p>0.1$). The 10 relocalizations of M5 were distributed randomly with respect to proximity of both water, farmland and buildings ($p>0.1$ for all). However, 8 of the 10 relocalizations were within 200 m of farmland.

Only the two individuals that dispersed more than 10 km were observed with prey. F3 killed a Cat *Felis silvestris catus*, a Mink *Mustela vison*, and an unidentified medium-sized mammal, probably a Squirrel *Sciurus vulgaris*. M5 killed 3 Hooded Crows *Corvus corone cornix* and a Hare *Lepus timidus*.

DISCUSSION

Dispersal

The recorded dispersal of the radio-equipped Eagle Owls (range 1.2-62 km, average 13 km, and median 2.8 km) is somewhat less than the dispersal found for ringed birds released from 1978-85, which ranged 0-354 km ($n=67$) with an average of 33 km and a median of 10 km (R.S. Larsen, unpubl.). This difference may have been negligible if we had managed to keep contact with the tenth bird, which probably dispersed out of the study area. Juvenile Eagle Owls released from captivity in Switzerland dispersed 0-400 km ($n=53$) with an average of 25 km (Glutz von Blotzheim and Bauer 1980). Hence, the results derived from recoveries of ringed released juveniles in south-east Norway and Switzerland agree well.

The direction of the dispersal of the five radio-equipped Eagle Owls that dispersed longer

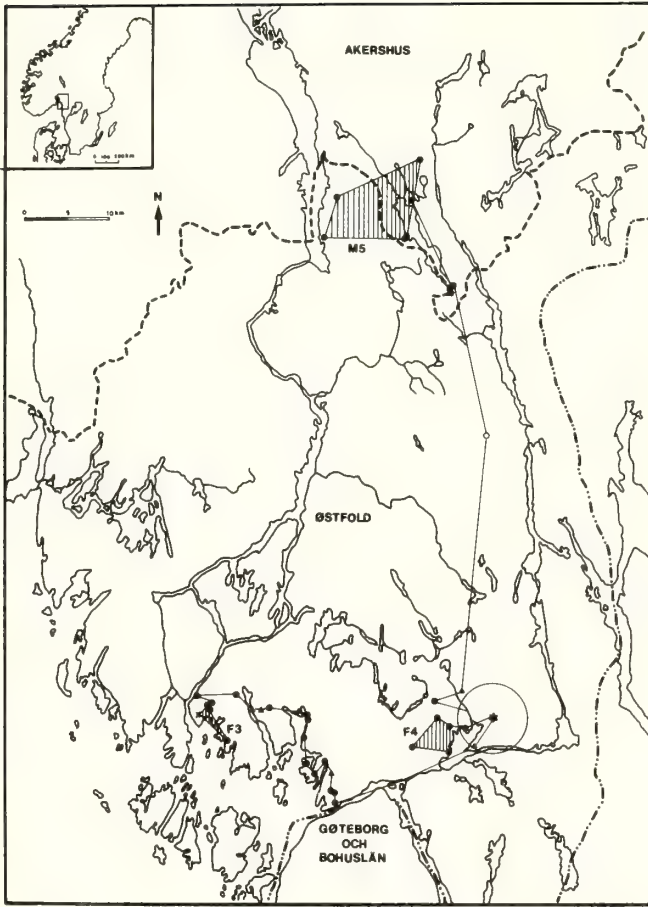


Figure 3.--Dispersal patterns of the three radio-equipped juvenile Eagle Owls that were tracked for more than 1 month. The asterisk denotes the release site, filled circles denote exact relocalizations from ground, open circles approximate relocalizations from air, open triangles approximate relocalizations from ground, and crossing denotes site of capture and new release after medical treatment of eye injury. Hatched areas denote home ranges. For more information see table 1.

than the median value was non-random, with a bias towards following natural guiding lines as lake and sea shores, and valleys with farmland, while avoiding larger areas of coniferous forest. On the other hand, recoveries of Eagle Owls banded as nestlings in the wild in Sweden were random with respect to direction (Olsson 1979), but the pooling of recoveries from a great number of nests may have swamped any direction biases from single nests.

Mortality

Within 12 weeks after release 78% of the radio-equipped juvenile Eagle Owls were dead. For birds ringed from 1978-85 in southeast Norway, 76% (n=66) died during the first 12 weeks (R.S. Larsen, unpubl.). Hence, mortality esti-

mates from radio tracking and ringing agree well.

Electrocution by power lines caused 57% of the recorded mortality of the radio-equipped Eagle Owls. Among the ringing recoveries of juvenile Eagle Owls released from captivity in southeast Norway, at least 52% (n=72) were reported as being due to electrocution (R.S. Larsen, unpubl.). The corresponding figure for juvenile Eagle Owls released in Sweden was 30% (Fremming 1987), for those released in Switzerland at least 27%, and for those released in West-Germany at least 20% (Glutz von Blotzheim and Bauer 1980).

Also for Eagle Owls ringed in the wild electrocution by power lines is an important mortality factor. It has been estimated at 16% in Norway and 20% in Sweden (Fremming 1987), at least 34% in Switzerland (Haller 1978), and at least 30% in both East- and West-Germany (Glutz von Blotzheim and Bauer 1980).

Juvenile Eagle Owls released in southeast Norway thus seemed to be more susceptible to electrocution by power lines than both wild Eagle Owls in Norway as well as both released and wild Eagle Owls elsewhere in Europe. The first difference may be explained by the fact that most ringing of wild Eagle Owls in Norway has taken place in more remote areas than the release of captive birds has. In addition, it spans a period of more than 25 years. The density of power lines in southeast Norway has increased markedly during this period (Fremming 1987).

The radio-equipped Eagle Owls were electrocuted when entering or leaving the poles, which they probably used as hunting perches. This phenomena is well known from North America, where large raptors living in open habitats are particularly vulnerable (Olendorff et al. 1981).

Habitat and prey

Of the two owls that dispersed greater than 10 km and are still alive, one preferred habitats near water. The other did not show any habitat preference. Both owls occurred as often as randomly expected near houses and other buildings, and thus did not show any avoidance of human settlements. This contrasts with what is known for wild Eagle Owls in Norway (Fremming 1987), and may be due to the fact that the radio-equipped birds were raised in captivity, and learned not to fear humans and buildings.

The prey recorded taken by the two owls fit well with what is known from Sweden about prey selection of Eagle Owls in areas with wetlands and farmland mixed with forest (Olsson 1979).

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Geographic Variations in the Diet of Eagle Owls in Western Mediterranean Europe¹

José A. Donázar²

The diet of the eagle owl changes from primarily rabbits in the Typical and Cold Mediterranean regions to a greater variety of smaller mammals in the Humid Mediterranean region. This tendency would lead to extinction in northern Mediterranean mountains.

INTRODUCTION

Since Geroudet (1965) pointed out the lack of information about the food habits of the Eagle Owl (*Bubo bubo*) in the European Mediterranean region, several articles have detailed the prey species of this strigiform, primarily in the Iberian Peninsula and the south of France. Because these food studies include the entire climatic regions of the occidental European Mediterranean, we have been able to use a multivariate analysis to determine taxonomic composition, species diversity, and variability in average prey size with respect to biogeographic changes.

MATERIALS AND METHODS

Following Aschman (1973), three climatic regions within the Occidental Mediterranean have been considered (fig. 1).

1. Typical Mediterranean. In the Iberian Peninsula it comprises the low-elevation regions with marine influence: Portugal, Extremadura, Andalusia, and the Levante coasts. In the south of France and north of Italy it includes only the Riviera area. Within this area, ample information about the diet of the eagle owl has been compiled (Hiraldo et al. 1975a, Vericad et al. 1976, Perez Mellado 1980).

2. Cold Mediterranean. It comprises the high inner regions from the Iberian Peninsula: Mesetas, Ebro Valley. Two works (Hiraldo et al. 1975a, Perez Mellado 1980) detail the diet of the eagle owl in this zone, to which our own data (Donázar 1986) on three localities from the Ebro Valley are added.

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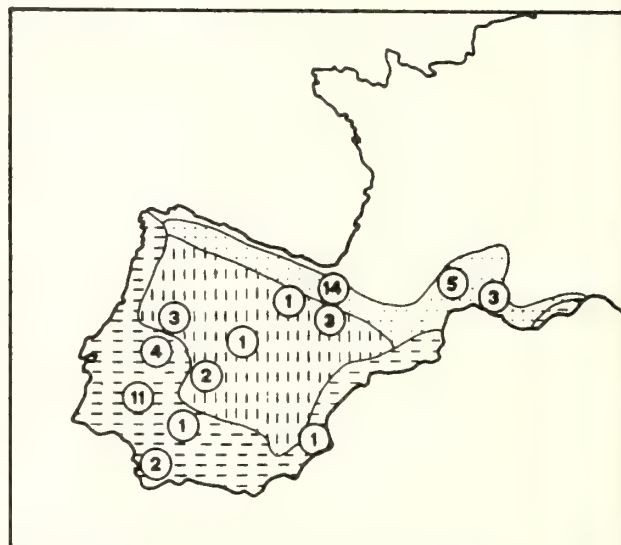


Figure 1.--Division of western Mediterranean Europe on the basis of climatic regions proposed by Aschman (1973). Horizontal dashes: Typical Mediterranean; vertical dashes: Cold Medit.; dotted: Humid Medit. Numbers indicate localities where eagle owl diets were analyzed.

3. Humid Mediterranean. It comprises the areas with Eurosiberian influence in the north edge of the Iberian Peninsula: Cantabric Mountains, Pyrenees, and in France, the Central Massif and the Provence. The diet of the eagle owl has been documented in several publications: Thiollay (1969), Choussy (1971), Schumacher and Lups (1975), Blondel y Badan (1976), Cheylan (1979), Cugnasse (1983), plus our own information about 14 locations from the southwest slope of the Pyrenees (Donázar op. cit.).

With this information, a data matrix has been constructed on the basis of 51 localities, all of which had more than 50 prey. For each locality, the appearance frequency (%) of the following prey

categories was extracted: ERI: Erinaceus europaeus; LAG: Lagomorpha; ARV: Arvicola sapidus; MIC: Microtinae (others); RAT: Rattus; MUR: Muridae (others); GLI: Gliridae; FSF: Falconiforms and Strigiforms; ALE: Alectoris rufa; COL: Columbiforms; COR: Corvidae; TUR: Turdidae; OTA: Other Birds; OTP: Other Vertebrates; INV: Invertebrates. A correspondence factorial analysis allowed us to represent both matrix sets in the same plane, and detect visually associations between location and prey category.

Trophic diversity (H') was calculated by means of the Shannon Index (see Herrera 1974, Jaksic and Marti 1984). The same prey categories defined for the correspondence analysis were considered. The function was calculated with e-log.

The Mean Weight of Prey (MWP) was estimated from bibliographic references (Geroudet 1965, Van de Brink and Barruel 1971, Hiraldo et al. 1975b), which give mean weights for mammals and birds. The rest of the prey weights were calculated from our own data.

RESULTS

The analysis generated three axes that account for 56.73% of the variance (table 1, figs. 2, 3). Axis I accounts for 39.43%, and defines a contraposition between Lagomorpha (in the negative zone) and Rattus and other Muridae (in the positive zone). Looking at the position of localities in the space defined by this axis, a clear bioclimatic gradient can be observed between the most meridional regions (Typical and Cold Mediterranean), where the eagle's diet is based on Lagomorpha (almost exclusively Oryctolagus cuniculus) with some Alectoris rufa, Columbiforms, and Invertebrates, and the Humid Mediterranean regions, where feeding is centered on small mammals.

The second and third axes account for lower proportions of the variance (10.81% and 6.49%), and denote the substitution of alternative prey for Rattus: Microtinae and birds in Axis II, and small Muridae in Axis III.

The localities characterized by a diet based on Rattus are different from a biogeographic point of view (Cold and Humid Mediterranean). Microtinae and birds tend to be the preferred diet in Humid Mediterranean areas of southern France, while the central European influence permits the appearance of social Microtus. On the other hand, the small Muridae (Mus spretus and Apodemus sylvaticus) characterize the diet in the humid regions of northern Spain (Pyrenees) and in a locality of southern France.

Both diet diversity and mean weight of prey show notable interregional variations, but both follow a precise pattern of decreasing MWP and increasing diversity (H') in the south-north direction as the places become colder and wetter

Table 1.--Results of correspondence analyses; contributions of prey categories to formation of each axis. See Methods for significance.

Factor	I	II	III
ERI	0.035	-0.246	0.178
LAG	-0.549	0.259	-0.077
ARV	0.092	-0.056	-0.002
MIC	0.095	-0.420	0.039
RAT	0.485	0.363	0.691
MUR	0.610	0.185	-0.619
GLI	0.031	0.048	-0.008
FSF	0.040	-0.177	-0.044
ALE	-0.129	0.022	-0.049
COL	-0.099	-0.067	-0.093
COR	0.081	-0.455	0.122
TUR	0.094	0.143	-0.199
OTA	0.060	-0.513	0.105
OTP	0.023	-0.032	-0.065
INV	-0.152	0.071	0.131
Variance (%)	39.43	10.81	6.49
Cum. Var. (%)	39.43	50.24	56.73

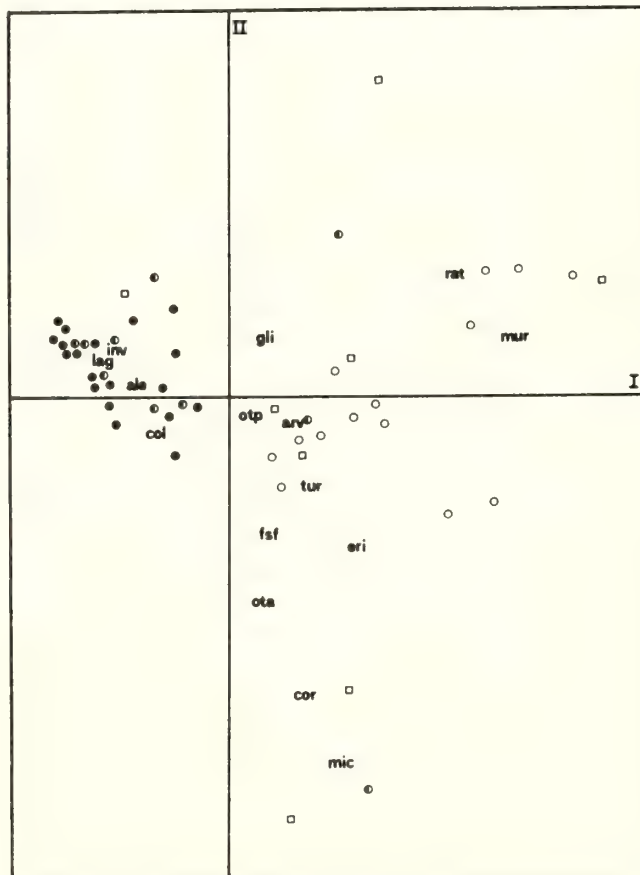


Figure 2.--Ordination of localities and prey categories on axes I and II. ●: Iberia, Typical Mediterranean; ○: Iberia, Cold Medit.; □: France, Humid Medit. region. See Methods for significance.

(table 2). The statistical significance of the interregional differences has been calculated by means of Student t-tests. The results (table 3) show that the Typical and Cold Mediterranean regions tend to be homogeneous between themselves, as do the two Humid Mediterranean subregions (Iberian and French). With respect to H', however, southern France tends to resemble the Cold and Typical Mediterranean regions, due perhaps to the proximity of certain sample areas (Provence) to the Riviera.

DISCUSSION

The close spatial association among localities in the Typical and Cold Mediterranean regions seems to be a logical result of the extraordinary abundance of rabbits in these ecosystems (Soriguer 1981), and consequently, their high food value for the eagle owl (Hiraldo et al. 1975a). This would lead to the trophic specialization of the owl, and thus the reduced diversity index and high average size of prey.

In Humid Mediterranean regions, however, the rabbit occurs in low densities with a fragmented spatial distribution (Cheylan 1979, Ceballos in prep.). This seems to induce the owl to complete its diet with prey of less food value: rats and

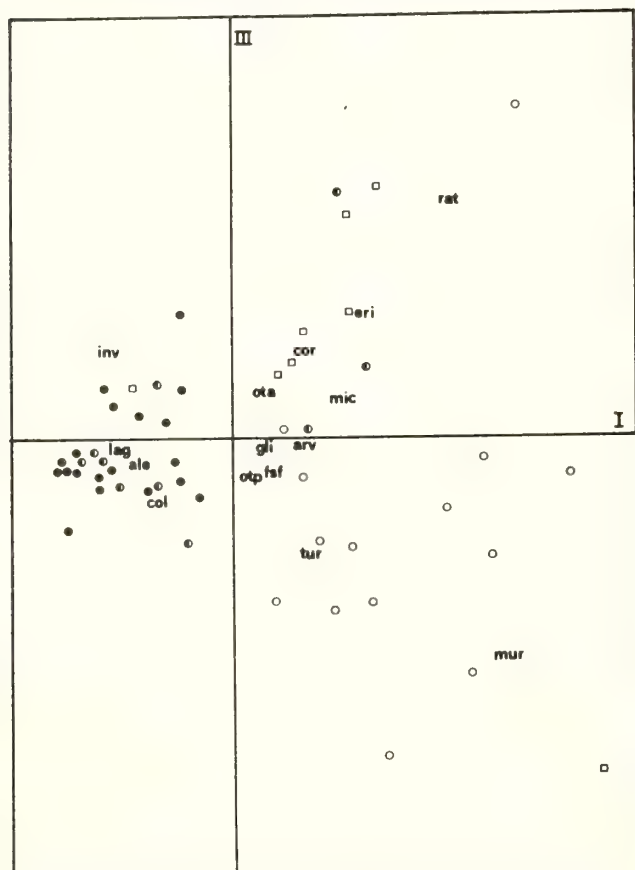


Figure 3.--Ordination of localities and prey categories on axes I and III. Symbols same as in fig. 2.

Table 2.--Values of trophic diversity (H') and mean weight of prey (MWP) in each region considered.

Region	H'	MWP	n
Iberia typical	1.209 (492.3)	889.2 (200.1)	19
Iberia cold	1.223 (433.9)	726.4 (233.4)	10
Iberia humid	1.842 (0.368)	395.9 (128.9)	14
France humid	1.715 (731.0)	515.5 (238.9)	8

Table 3.--Values of Student t-tests in comparisons among climatic regions with respect to H' and MWP. ns: not significant; x: $p < 0.05$; xx: $p < 0.01$; xxx: $p < 0.001$.

Iberia cold	Iberia humid	France humid	H'
0.756 n.s.	4.045 xxx	2.108 x	Iberia typical
	3.772 xx	1.779 n.s.	Iberia cold
		0.547 n.s.	Iberia humid

Iberia cold	Iberia humid	France humid	MWP
1.969 n.s.	8.060 xxx	4.193 xxx	Iberia typical
	4.454 xxx	2.827 x	Iberia cold
		1.538 n.s.	Iberia humid

small Muridae. The main substitution prey, the brown rat, has a biomass theoretically very appropriate to the strigiform needs (Donazar 1986) since it fulfills the dietary requirements of the owl (see Glutz von Blotzheim and Bauer 1980). Nevertheless, its presence in the diet is limited to a few localities with no biogeographic connection. This can be due to the fact that the rodent has an irregular spatial distribution, being mostly linked to human developments (Perez Mellado 1980, Real et al. 1985, Donazar 1986).

That would force the eagle owl to feed on smaller animals, primarily Microtinae and small Muridae.

One of these species, Mus spretus, can reach 40% of the owl's captures in some Pyrenean localities (Donazar 1986). This contradicts opinions of other authors (Jaksic and Marti 1984, Orsini 1985), who consider improbable the capture of this small mammal, very common in the western European Mediterranean region, because of its low body weight (not more than 20 g.). Our data tend to indicate that Mus, like other small mammals, is preyed upon by eagle owls on the basis of availability of prey of greater food value (Pyke 1977), as is the case with other birds of prey (Davies 1977, Goss-Custard 1977, Krebs et al. 1977).

The substitution of small mammals for rabbits leads to an increase in prey diversity and decrease in mean weight of prey toward the Humid Mediterranean region. This tendency is a common phenomenon for large predators on the Iberian Peninsula: Aquila chrysaetos, A. adalberti, Hieraetus fasciatus, Lynx pardina (Caldron et al. 1980, Delibes 1980, Alamy et al. 1984, Garzon et al. 1984). The eagle owl thus differs from other European strigiforms, which tend to fluctuate rapidly in Typical Mediterranean regions when rodents are scarce (Herrera 1974, Delibes 1975, Manes 1983).

This progressive substitution of smaller prey can lead to a loss in hunting efficiency, which can cause an energy deficit if the eagle's larger prey are scarce and the energy costs of searching for and capturing smaller prey exceed their food value (see Valverde 1967, Schoener 1971). This opinion is substantiated by the fact the eagle owl was partially extinct in certain Humid Mediterranean areas (Pyrenees of Navarre, French Central Massif) due to the epizootic disease, mixomatosis, which caused the virtual disappearance of the rabbit (Choussy 1971, Purroy 1974). The subsequent recovery of the rabbit population was followed by expansion of the eagle owl range to recover part of the lost area (Bergier y Badan 1979, Cheylan 1979). This seems to indicate that, in the absence of large prey, the eagle owl is unable to survive on a diet based exclusively on small mammals. Thus the mountains of northern Mediterranean regions have a notable parallelism with the nordic ecosystems (taiga) where, in some areas, the eagle owl similarly consumes a large proportion of small rodents and has suffered population losses conditioned by the disappearance of some larger prey species (Olsson 1979, Myrnerud and Dunker 1983).

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Addled Eggs in Great Horned Owl Nests in Saskatchewan¹

C. Stuart Houston,² Roy D. Crawford,³ and Donald S. Houston⁴

Abstract.--In visits to 1716 nests of the Great Horned Owl, addled eggs were present in from 1.2 to 9.3% of successful nests, and in another 11 nests without young. Addled eggs (4 of 5 opened contained identifiable dead embryos) were most common in years of poor reproductive success.

INTRODUCTION

Comprehensive studies of reproductive failure in domestic fowl, a matter of great economic importance, have been carried out for over 100 years. A landmark paper by Riddle (1930) studied doves, pigeons and domestic fowl and reported that the embryos of all showed "two distinct periods of high mortality ... very early in development and ... very near the end of incubation." After a detailed list of possible causes of embryo death, Riddle concluded that thick shells, "the very device ... utilized by eggs to prevent water-loss--and avoid death in the final period--may too greatly affect respiratory exchange and thus cause death in the early period." Insko and Martin (1935) found that for White Leghorn chick embryos, the peaks of mortality fell on the 2nd and 19th days of a 21-day incubation and for Bronze Turkey embryos on the 4th and 25th days of a 28-day incubation.

Ricklefs (1969) reported that the incidence of unhatched eggs averaged 8% in six species of passerine birds. Little has been written about this problem in North American raptors. The incidence of unhatched eggs of the Red-tailed Hawk, Buteo jamaicensis, Northern Goshawk, Accipiter gentilis, Prairie Falcon, Falco mexicanus, and Screech Owl, Asio otus, has been reported as 4%, 10%, 11%, and 18%, respectively (Luttitch et al 1971; McGowan 1975; Ogden & Hornocker 1977; Klaas and Swineford 1976).

We studied hatching failure in the Great Horned Owl, Bubo virginianus, as measured by the frequency of addled eggs encountered during visits to 1727 active nests in Saskatchewan. Hatching failure (Ricklefs 1969) can result from:

1. Infertile eggs
2. Death of initially viable eggs (usually early in incubation)
3. Death of a fully-formed chick at or during hatching.

[Nest failure with egg loss, beyond Ricklefs definition of hatching failure, can also result from death of the adult owls, desertion (Southern 1970) or predation (Lundberg 1985), but in owls it should rarely be due to parasitic infestation, nest site competition or severe storms, and never to brood parasitism.]

We follow standard dictionaries in equating addled and rotten as synonymous. We do not have enough data to be as specific as Campbell and Lack (1985) who, without citing any authority for their decision, define an addled egg as one "in which the developing embryo has died, as opposed to an infertile egg in which no development has taken place." Although we presume that an infertile egg would "dry down" rapidly during incubation and might break before fertile eggs had hatched and before bacterial growth could proceed to the "slosh" stage, we nevertheless have only preliminary evidence to suggest that most or all addled eggs represent embryo death.

METHODS

The senior author and his many volunteer assistants have recorded presence or absence of unhatched eggs during visits to raptor nests since 1966. Eggs in nests with tiny young were not disturbed, since hatching is staggered in owls and such eggs may have been viable. If the smallest nestling was one week or more old, the egg was shaken. Eggs that had an audible "slosh" from air and fluid content (indicating cell death, autolytic breakdown of membranes, mixing of liquefied yolk and white, and secondary bacterial overgrowth), were classed as addled and taken from the nest.

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TABLE 1 - YEARLY VARIATION IN ADDLED EGGS IN GREAT HORNED OWL

Year	Nests	Yg	Ratio	Percent	#N	OY	OY	OY	1Y	1Y	1Y	2Y	2Y	3Y
						with	1e	2e	3e	1e	2e	1e	2e	1e
						ad	e							
1966	51	116	2.27	3.92%	2				2					
1967	110	255	2.32	3.64%	4		1		0	1		2		
1968	163	401	2.46	3.07%	5				2			2		1
1969	85	224	2.64	1.18%	1							1		
1970	113	282	2.50	1.77%	2				1			1		
1971	62	132	2.13	3.23%	2	1			1					
1972	76	167	2.20	6.58%	5		1		2			2		
1973	27	49	1.81	3.70%	1				1					
1974	38	65	1.71	5.26%	2				1			1		
1975	69	145	2.10	7.25%	5	1	2	1	1					
1976	54	107	1.98	9.26%	5		1		2			2		
1977	67	151	2.25	2.99%	2							2		
1978	81	191	2.36	1.23%	1									1
1979	84	211	2.51	3.57%	3				1			2		
1980	65	116	1.78	4.62%	3		1		2					
1981	148	374	2.53	4.73%	7				3			1	1	2
1982	80	157	1.96	3.75%	3				1	1		1		
1983	101	208	2.06	1.98%	2				2					
1984	103	197	1.91	3.88%	4	1			3					
1985	55	106	1.93	7.27%	4	1			2			1		
1986	84	207	2.46	5.95%	5				1			3	0	1
TOTAL	1716	3861	2.25	3.96%	68	4	6	1	28	2	0	21	1	5



Great Horned Owl attacking Houston
(Photo, Hans S. Dommasch)

Until 1985, all addled eggs were frozen and sent to the Canadian Wildlife Service (CWS) in Ottawa at the end of the season. Few of these eggs have been analysed chemically, but they have been kept frozen in a reference collection, available for possible retrospective study of pesticide content and egg shell thickness, should data from that period or location come to be of interest.

In 1986 we attempted for the first time to determine whether an addled egg indicated embryo death or infertility. Only in this one year were eggs candled, then broken and examined in Saskatoon. (Frozen eggs in the CWS repository are unsuitable for candling).

The number of nests found each year varied greatly (27-163), in spite of approximately constant effort by a group of farmer friends with a special knack for finding owl nests. At the low point in the cycle of the Snowshoe Hare, *Lepus americanus*, most owls moved away, and of those remaining, less than half made any attempt to nest (Houston 1975b).

Because of the unusually wide variability in breeding activity and success in this species, it is inadequate merely to plot the number of addled eggs encountered each year. Hence the number of addled eggs was compared to the number of successful breeding pairs and to the total number of eggs produced each year.

RESULTS

Between 1966 and 1986, inclusive, the senior author visited 1727 Great Horned Owl nests with eggs or young. Of these, 1716 successful nests produced one or more young to banding age; the other 11 occupied nests contained only addled eggs. Altogether there were 79 addled eggs in 68 nests, involving 4% of all nests and 2% of all eggs. The frequency of nests with addled eggs ranged from a low of 1.2% of nests in 1969, the year with the highest number of young fledged per successful nest, to a high of 9.3% in 1976, a year of below-average breeding success (Table 1).

Of the eleven nests which had addled eggs only, without young, four had one addled egg, six had two, and one had three. Four of the 11 nests with addled eggs but no young were found in 1975, a year of low owl production. Of 57 nests with addled eggs and live young, the most frequent combination was one addled egg and one live owlet (28 nests), followed by one addled egg with two live young (21 nests). Three nests with young owls contained two addled eggs each (Table 1).

Addled eggs feel cool to the touch, indicating lack of recent incubation, and are well preserved during cool weather in April and May. Eggs of ducks, coots and upland game, brought to the nest in the oviduct of prey species, are also well preserved in owl nests (Houston 1975a). In contrast, hawk eggs found in midsummer are often

exposed to ambient temperatures as high as 40° C. Excessive decomposition and bacterial overgrowth may make it impossible to detect embryonic remnants (Houston, Fox, Crawford, Oliphant, mss.)

In 1986, the only year in which owl eggs were sacrificed for direct examination, three contained a small embryo, indicating failure early in incubation. One contained a fully formed dead embryo with pinfeathers and a prominent egg tooth. One egg contained no recognizable embryonic material.

The years with the most nests and most eggs per nest were the years with the lowest proportion of addled eggs, while years of fewer nests and fewer eggs per nest had a higher proportion of addled eggs. Regression analysis reveals a significant negative correlation ($p < 0.01$) between the percentage of addled eggs and the number of young per nest (Figure 1). This correlation is only moderately strong, with an r value of 0.51. In a year of below-average owl success (Houston 1971), the increased percentage of addled eggs is only one of the measures of poor reproductive performance.

DISCUSSION

In spite of early nesting under extreme climatic conditions, and cyclic variability in numbers of its main prey species, the Great Horned Owl has an unusually low incidence of addled eggs. However, there is a significant inverse relation between the annual proportion of addled eggs and the average number of young produced per successful nest that year -- which in turn is related to food availability. This is a natural phenomenon; given a herbivorous prey species in late winter, there is little potential for accumulation of biocides.

Brief interruptions of incubation, obligatory even in the coldest weather, cause no harm because "the avian blastoderm is capable of withstanding a relatively severe degree of cold" (Romanoff). We have not observed any obvious correlation with inclement weather, but we have not done regression calculations against weather variables such as temperature and snow depth. In fact, we have observed a Great Horned Owl incubating two eggs successfully through temperatures as low as -34 C. (Houston 1965). We hypothesize that a normal degree of cold might have adverse consequences only in years when the male brings insufficient food to the incubating female who is thereby forced to leave the nest for longer than normal periods to obtain food for herself.

Results from random visits to owl nests are not directly comparable to results of poultry science research. In the laboratory, a failed egg is studied before decomposition sets in. In the field, the addled egg that "sloshes" teems with bacteria; decomposition may have been under way for many weeks. Nevertheless, our small sample of five rotten eggs in 1986 suggests that such eggs are more commonly the result of embryo death than infertility. We encountered three instances of

early and one of late embryo death, roughly consistent with the classic studies in domestic fowl.

It is our working hypothesis, supported by our small sample in 1986, that addled Great Horned Owl eggs represent embryonic death with secondary infection, not primary infection or infertility. When death of the embryo occurs, there is immediate failure of the normal bacteriostatic and immunologic mechanisms of the live organism; diversified microorganisms already residing on or even in the eggshell soon proliferate in the excellent culture medium. In poultry, fertile and infertile eggs are contaminated about equally (Romanoff and Romanoff 1949).

Other Long-term Studies

Our inverse relationship between addled eggs and food availability is consistent with the only other long-term studies of variation in the incidence of addled raptor eggs, from Europe. In the Buzzard, Buteo buteo, addled eggs constituted 5% of all incubated eggs in good food years and 15% in poor ones (Mebs 1964). In the Tawny Owl, Strix aluco, the loss of 115 of 279 eggs was ascribed to "desertion and chilling" and was most frequent when the female left her nest because food supplies were scarce (Southern 1970). Our results agree with the prediction of Lundberg (1985) that, given a low daily risk of predation, a larger clutch size should accompany increased food availability. On the other hand, our results are contrary to Lundberg's other prediction, on evolutionary grounds, that low predation and increased clutch size might be accompanied by a higher rate of egg failure.

Usefulness of this information

Knowledge of the average and range of extremes of frequency of rotten eggs should help to understand relationships between reproductive success and food availability. In some species it might also prove useful in early detection of biocide effects, since some biocides increase the risk of reproductive failure (Newton and Bogan 1974). Differentiation between chemicals causing infertility and those causing early or late embryo death might be important.

Our retrospective data, collected incidental to a long-term banding effort, point to the need for more detailed studies, including histologic examination of dead embryos. We encourage others to take an interest in this neglected area.

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Some Features of Long-Eared Owl Ecology and Behavior: Mechanisms Maintaining Territoriality¹

Vladimir I. Voronetsky²

Abstract.--Territorial behavior of 48 pairs of Long-eared Owls was studied for 14 years in an area 60 km west of Moscow. All members of an owl family--male, female and young--play a role in territorial defense. The complex behavior and vocalizations exhibited by parents and their offspring changes during the breeding season. This unusual territorial defense system evidently ensures greater hunting and breeding success in the Long-eared Owl, which has specialized food habits and is highly nocturnal.

The territorial behavior of 48 Long-eared Owl (*Asio otus*) families was studied for 14 seasons in the Moscow area (60 km west of Moscow). In the biotope inhabited by the families, tape recordings or imitations of other owls' voices were periodically played or given and adult or young owls were exhibited.

Territoriality in this species is ensured by complicated behavioral mechanisms supported by all members of the family. The male, the female and the young at different stages of the breeding period manifest various territorial-defensive reactions using polyfunctional acoustic signals or series of signals. The behavioral patterns maintaining territoriality in general can be described as follows:

1. Territorial males in the early breeding stage are actively vocalizing. Their low-frequency acoustic signals (Fig. 1), strengthened by demonstrative flights and wing-clapping, are well known. The effect of this behavior is later enhanced by the female who exchanges calls with the male and moves across the habitat clapping her wings in flight like the male. Thus, territorial behavior during the display period comprises a set of acoustic signals and demonstrations by male and female. The wide variety of signals used by the Long-eared Owl ensure the necessary reliability of this form of signal in the unsteady

spring weather conditions when the environment is saturated by low-frequency noises.

2. With the beginning of incubation the intensity of demonstrations on the territory sharply decreases. One to two weeks after the beginning of egg-laying the males as a rule have ceased displaying and do not respond to other

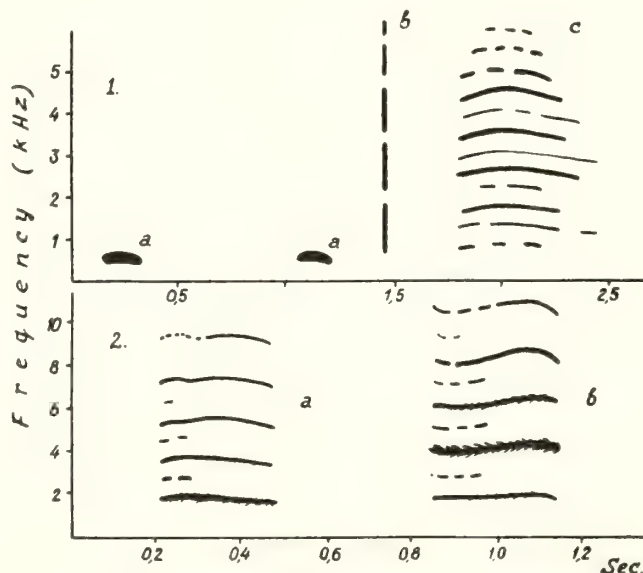


Figure 1.--Sonograms of display acoustic signals: male hooting (a), wing-clapping (b) and female call (c).

Figure 2.--Sonograms of young owls' polyfunctional acoustic signals in normal condition (a) and aggression (b). Fundamental frequency is shifted to the higher range of acoustic spectrum.

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males' voices. At this time they defend only one part of their territory--the hunting area. Incubating females become more and more indifferent to male display signals, but increasingly aggressive to voices of other females (Fig. 2) and strange owlets. In this situation, females show a wide range of reactions--from irritated cries upon the nest to direct aggression and chasing accompanied by a large repertoire of aggressive signals. This pattern of female behavior is maintained during the whole period of feeding of the young by the mother, but it declines as soon as the fledglings become fully capable of flying.

3. Young owls, along with the development of the acoustic signals, show behavioral reactions from approximately 2 weeks of age that function in maintenance of the territory. The nestling feeding call acquires polyfunctional significance and can serve as a reliable territorial marker. Probably it is the reason why such signals have unexplainably high intensity. The nestlings react to the appearance of a strange brood near the nest by increasing the intensity of their calls and producing them more often, while the fundamental frequency of the signals is shifted to the higher range of the acoustic spectrum (Fig. 3). In the same situation the fledglings show similar vocal alterations. In addition, they actively seek the source of sounds and try to approach it. The aggression of the young is usually supported by the female. Their collective attacks on intruders at the territorial border continue until the strange brood leaves the host territory.

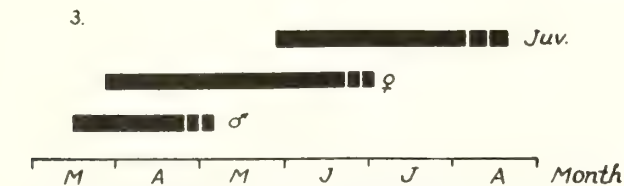
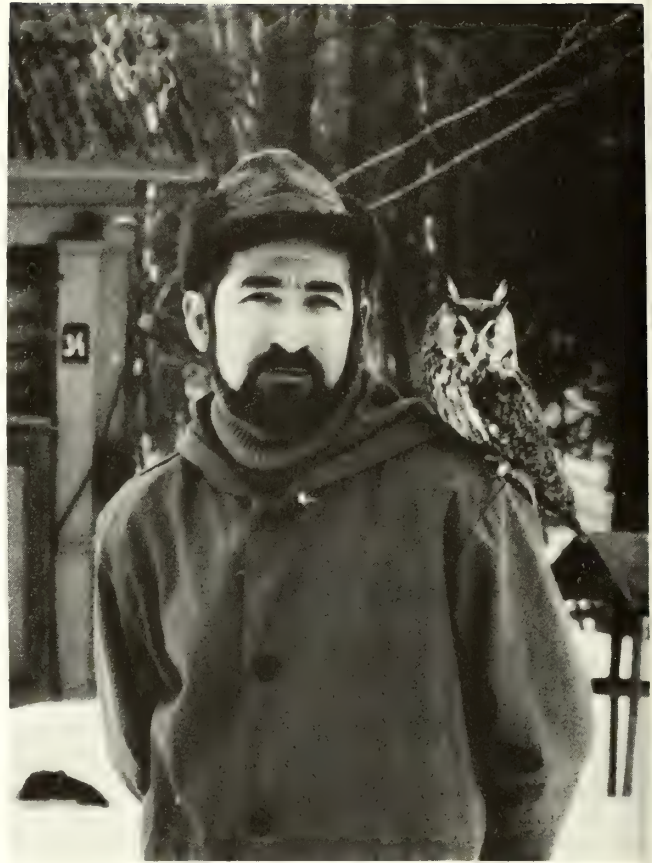


Figure 3.--Vocalization time periods of different members of the brood during the breeding season.

4. Towards the end of the nesting period, the intensity of the female and fledgling reactions to intruders steadily decreases. It enables some young owls that have not yet been fed by their parents to approach the intruding family groups



Voronetsky and a long-eared friend.

and to beg food from the strange parents. It is especially important during the period when independent hunting by the young is difficult because of prolonged rains or strong winds.

Thus, the complicated system of territorial defense in the Long-eared Owl, while being extremely individually variable, is ensured by the optimal distribution of functional roles between the members of the family during the whole breeding period. Such a system evidently provides greater hunting and breeding success in this species which is specialized for a nocturnal life strategy and practically strict myophagia.

Food and Food Ecology of the Long-Eared Owl in an Agricultural Area¹

Josef Kren²

Artificial perches installed in an intensively exploited agricultural area were heavily used by Long-eared Owls. Primary prey species, determined by analysis of pellets beneath the perches, were Common Voles and other species regarded as major agricultural pests. The nature of the prey indicates a narrow food spectrum related to the monoculture.

The present paper is a partial result of a food ecology study of two of our most common owls, the Long-eared Owl and the Tawny Owl, in an intensively used agricultural landscape. Even though the food ecology of the Long-eared Owl has been dealt with by many writers, both in Czechoslovakia and in other European countries, these problems have been very topical in connection with the possibility of utilizing birds of prey in the integrated protection of agricultural monocultures.

In Czechoslovakia the food of the Long-eared Owl was studied in detail--on the basis of pellets by Farský (1928), Folt (1956), Zelený (1961), Boháč and Michálková (1970) and Bejček (1980). The material processed by them came from different environments.

I have analysed 682 pellets collected at four sites in South Moravia (Czechoslovakia). All sites were located in an intensively exploited agricultural area and were similar in all respects. An important element of this landscape were freely scattered groups of trees and shrubs of different ages which, however, did not constitute continuous stands. The sites near the village of Kostelany (denoted as "C") are situated in a close neighbourhood of a flood-plain forest. The remaining sites are denoted: ("A") near the village of Holní Némč, ("B") near the village of Hluk, and ("D") near the village of Traplice.

Pellets were collected under T-shaped perches installed in alfalfa fields to support the predation activity of birds of prey for the purpose of controlling small rodents. In autumn of 1982 and 1983 temperatures were normal.

In 682 analyzed pellets skeletal remnants of 1368 animals were found belonging to the classes Aves and Mammalia. Mammals were represented by five species, the number of skeletal remains belonging to 1357 individuals, which constitute the main part of the prey. The most common species was the Common Vole (*Microtus arvalis*) whose percentage representation for the 2 years was 90.3%. The second most numerous representatives were Mouse species (*Apodemus* sp.). Their total share in the 2 years was 5.7%. Bank Vole (*Clethrionomys glareolus*) was represented by 1.8%, House Mouse (*Mus musculus*) by 1.1%. In isolated cases there occurred Common Shrew (*Sorex araneus*).

Birds found in the pellets were not determined to species. They were representatives of the order Passeriformes. Their share in the prey was 0.8%. The share of the individual food components in the pellets is given in detail in Table 1.

No remains of invertebrates were found in the pellets. In 1982 the mean number of vertebrates found in the pellets varied between 1.4 and 2.2 vertebrates per pellet. In 1983 these values varied from 1.7 to 2.6 vertebrates per pellet. These values for the individual sites are given in detail in figures 1 and 2.

For judging the food requirements of the Long-eared Owl I used Shannon's Formula (H) according to Pielou (1969). The value of Shannon's formula is--in the sum for the 2 years--0.3823 at the evenness index of 0.2133. The values for the individual years are given in Table 2.

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Table 1. Contents of Long-eared Owl pellets from all sites.

item	year					
	1982		1983		1982+1983	
	n	%	n	%	n	%
<i>Microtus arvalis</i>	611	87.9	625	92.8	1236	90.3
<i>Apodemus</i> sp.	41	5.8	38	5.6	79	5.7
<i>Clethrionomys glareolus</i>	19	2.7	6	0.8	25	1.8
<i>Mus musculus</i>	16	2.3	0	0	16	1.1
<i>Sorex araneus</i>	0	0	1	0.1	1	0.07
Aves	8	1.1	3	0.4	11	0.8
total	695	99.8	673	99.7	1368	99.7

Table 2. Shannon's index and Evenness index for contents of Long-eared Owl pellets.

	year		
	1982	1983	1982+1983
H'	0.4735	0.2941	0.3823
E	0.2942	0.1827	0.2133

The most important part of the prey consisted of Common Vole and Mouse species. These are the most common species in the agricultural areas of the given region and also are the chief pests.

A high percent of Common Voles in the diet of the Long-eared Owl was found by most authors: Bejček (1980): 86.29%; Boháč and Micháľková (1970): 93.10%; Folk (1956): 97.94% for Moravia and 72.60% for Slovakia; Vondráček (1985) 85.10%. These data on the whole correspond to the values found by me. Mice are also listed by Bejček (1980) and Vondráček (1985) as the second most frequent item, but in Bejček the value of percentual representation is twice as high. Bank Voles occurred in pellets at site "C" which is situated in the neighbourhood of the plain forest where the population level of this species is relatively high. Bejček (1980) and Vondráček (1985) did not find Bank Voles in pellets. Folk (1956) writes that the occurrence of this species in the diet of the Long-eared Owl is low.

In the 2 years studied there was a clear supremacy of representatives of the family Microtidae--1261 specimens (92.99%) over representatives of the family Muridae--95 specimens (7.0%).

Figure 1. The mean number of vertebrates in a pellet.

A - site near the village of Dolní Němčí.
B - site near the village of Hluk.

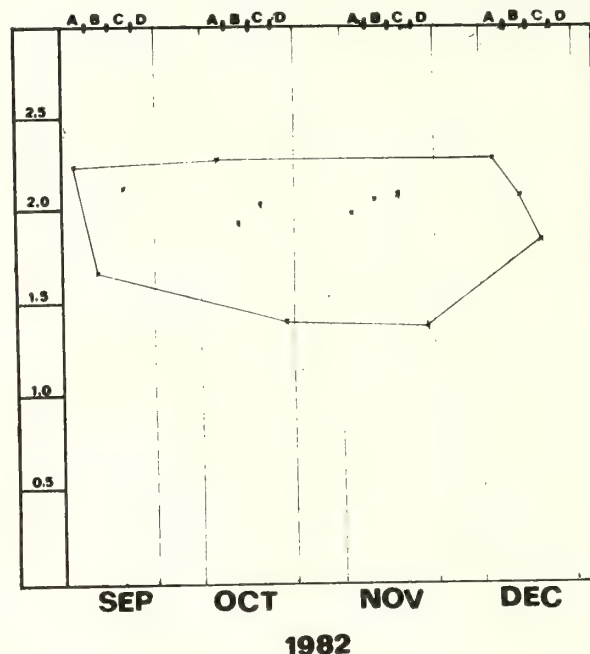
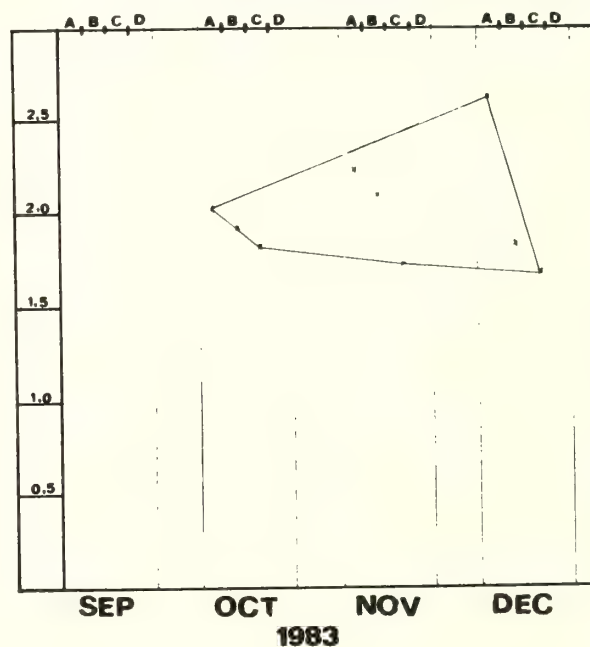


Figure 2. The mean number of vertebrates in a pellet.

C - site near the village of Kostelany.
D - site near the village of Traplice.



In the opinion of most authors, birds are relatively important in the food of the Long-eared Owl, which was also reflected in my results. The situation is, however, changed in bad weather or during the winter season (Bejček 1980), particularly when owls are concentrated in so-called

winter societies. The above authors show a relatively narrow food spectra for the Long-eared Owl during autumn and winter, but, despite that, the number of food components found in the pellets reaches higher values than those in my case. The very low value of Shannon's formula (0.3823) indicates stenophagy and specialization of the Long-eared Owl to one type of prey. Bejček (1980) found almost twice as high values of Shannon's formula (0.7342) as I at the evenness index of 0.2447.

On the basis of data from the literature, I calculated Shannon's formula (0.6323) and the evenness index (0.2637) from the food found by Vondráček (1985). Different values of Shannon's formula are, in my opinion, due to the effect of the station where the pellets were collected, because the share of the individual food components is directly proportional to the species available in a given environment.

The original reason for the installation of T-shaped wooden perches was to encourage predation activity by birds of prey in selected fields, especially Buzzard species and the Rough-legged Buzzard. Among the collected pellets the highest numbers were those of Long-eared Owls. This means that these artificially installed devices are used by this owl in its hunting strategy.

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Fidelity to Territory and Mate in Flammulated Owls¹

Richard T. Reynolds² and Brian D. Linkhart³

Abstract.--Adult flammulated owls were banded on a 452-ha area in Colorado. Nine adults nested 1 year only, five nested in 2 years, four in 3, one in 4, and one in 5. Males had a lower return rate than females. Once males established breeding territories, they returned to them each year. Females sometimes changed territories, and their corresponding dispersal distance (474 m) was similar to the mean distance across territories, 424 m.

INTRODUCTION

Fidelity to a mate or nesting site is widespread among birds, but is particularly common in adults of migratory species that return to breed in the same general area year after year. Fidelity to sites and mates has been studied in some charadriiformes (Wilcox 1959, Lenington and Mace 1975), passeriformes (Delius 1965, Darley et al. 1971, Harvey et al. 1979), seabirds (Coulson 1966, Richdale and Warham 1973, Ollason and Dunnet 1978), and falconiformes (Newton and Marquiss 1982). Little is known, however, about mate and site fidelity in strigiformes, particularly in migratory species.

In general, studies of birds show that males have greater fidelity to territories than do females, and that both males and females more often change territories and mates after a breeding failure than after a success (Greenwood 1980). Harvey et al. (1979) suggested that site fidelity is more likely in species that occupy stable environments, and that mate fidelity is more common among longer-lived species.

We report the annual rate of return to breeding territories, the duration of the pair bond, the frequency of reoccupancy of territories, and the breeding dispersal of flammulated owls nesting in Colorado. Although

we know of no recaptures of banded flammulated owls during migration or in winter, there is extensive evidence that this species is migratory (Jacot 1931, Phillips 1942, Phillips et al. 1964, Sutton 1960, Banks 1964, Phillips et al. 1964, Wolfenden 1970, Hubbard 1972, Balda et al. 1975).

STUDY AREA

This study was conducted on 452-ha of the Manitou Experimental Forest, Teller Co., in central Colorado. The forest on the study tract consisted of open old-growth (200+ yr) stands of ponderosa pine (*Pinus ponderosa*)--Douglas-fir (*Pseudotsuga menziesii*) on south- and west-facing slopes, dense younger (< 100 yr) stands of Douglas-fir--blue spruce (*Picea pungens*) on north aspects, and mixed quaking aspen (*Populus tremuloides*) and blue spruce in the drainages. Elevations ranged from 2550 to 2855 m, with ridges rising 100 to 250 m from bottoms. Trees had not been harvested on the tract since the 1880's (light selective cutting for railroad ties), and snags and cavity trees were relatively common on all slopes (Reynolds et al. 1985). Reynolds et al. (1985) and Reynolds and Linkhart (this volume) described the topography, vegetation, and soils on the study tract.

METHODS

Twenty-one adults were banded on the study tract during 5 nesting seasons (1981-1985). In addition, 9 nestlings were banded in 1981, 9 in 1982, 9 in 1983, 10 in 1984, and 15 in 1985. Three pairs and their nestlings from nests outside of our study tract were banded also. A suite of behavioral characteristics was used to identify the sex of individuals: males by their territorial, courtship, and copulatory behaviors, and high level of activity during nesting; and females by their recipient role in courtship feeding, food-begging behavior, and low level of

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activity during nesting (Reynolds and Linkhart 1984).

Each spring and summer, we searched the entire study tract and some of the surrounding forest for territorial males (Marshall 1939, Winter 1971). Nesting territories and home ranges were identified by marking territorial song trees (Reynolds and Linkhart 1984) and by radio-telemetry (Linkhart et al. in review). Once the boundaries of territories were known, all suitable nest cavities within territories were examined for nesting activity. Because our searches were intensive, we are confident that all nesting pairs and unpaired, territorial males on the study tract were found. All owls except for one pair (A18) and several unpaired, territorial males were captured and banded. We define "territory" as that area used exclusively (Schoener 1968) by a pair or by an unpaired, territorial male. By this definition, because there was no overlapping use of home ranges among flammulated owls (Linkhart et al. in review), home range for this species is synonymous with territory.

Our early spring surveys showed that adult males arrived and established territories during the first week of May (Reynolds and Linkhart this volume). Some females arrived at the same time, but the arrival period of females was longer. For example, we followed an unpaired female as she passed through the tract from south to north giving food solicitation calls on 20 May 1982. Another female was first found on 8 June 1981 in what appeared to be the early stages of pair formation with a previously unattached, territorial male. If young males continued to arrive through May, their arrival went undetected. As many as 6 nesting territories and 3 nonnesting territories on the study tract were occupied by males by the third week of May each year.

The nesting history of 20 of the 21 adults banded during this study was determined. Nine adults nested one year only, 5 returned and nested for two years, 4 for three years, 1 for four, and 1 for five (table 1). Males returned less often than females; banded males returned an average of 1.75 years, while females averaged 2.38 years. The maximum number of seasons an owl returned to nest was 3 years for males and 5 years for females. No birds banded on our tract as nestlings returned to nest or were ever recaptured in subsequent years.

The maximum number of years adults remained paired to the same mate was 3; 10 pairs nested together only 1 year, and 1 pair remained paired for 2 and 1 pair for 3 years. The occupancy of nine nesting territories (MN1 was outside the study tract) through the 5-year study followed a different pattern. One territory was occupied for a single year, three were occupied for 2 years, four for 3 years, and one for 5 years (fig. 1).

Table 1.--Number of years banded flammulated owls nested on the study tract in 5 years, 1981-1985.

Years	No. of males	No. of females	Total
1	6	3	9
2	3	2	5
3	3	1	4
4	0	1	1
5	0	1	1

On six of the nine nesting territories, either the adult male or the female (in one case both adults) was replaced by a new male or female once or twice during the 5-year study (table 2, fig. 1). In none of these cases did an adult male move from one territory to another within our study tract--each replacement male

YEAR	TERRITORY									
	A39	A15	A4	A24	A29	A12	A10	A18	A11	MN1
1981	M-F		M-F	M-F	M-F	M-F	M	M-F		
1982		M-F	M-F	M-F	M-F	M	M-F	M		M-F
1983			M-F	M-F	M-F	M		M	M-F	M-F
1984		M-F		M-F	M-F	M-F		M-F	M-F	
1985	M-F			M-F	M-F	M-F		M	M-F	

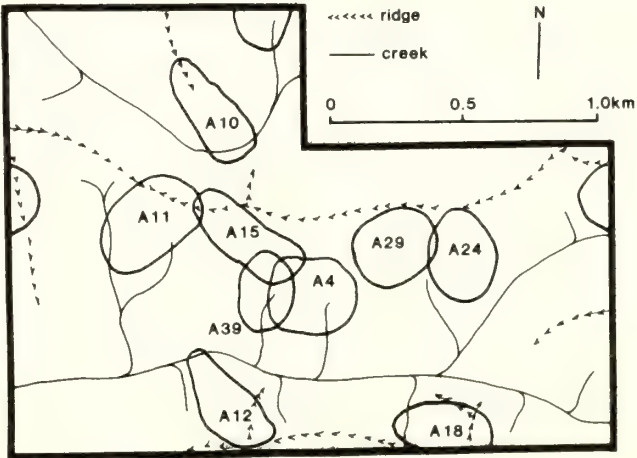


Figure 1.--Fidelity to mate and territory, female breeding dispersal, and schematic of study tract showing approximate boundaries of territories. Unmarked peripheral territories were occupied by unidentified male owls. Territory MN1 did not occur on tract (see text).

was unbanded. In contrast, 4 of the 7 female replacements were banded adults that had nested elsewhere on the study tract in a previous year. In one case, a female (originally A39) nested 3 consecutive years on the tract in different but adjacent territories (fig. 1). In another case, two females (originally A29-83 and A15-84) nested with a male on his (A12) territory in 2 consecutive years (female A29 in 1984 and female A15 in 1985). The overall replacement rate (total replacements per year for all territories) was 22.2% for males and 38.9% for females. Thus, even though males have a lesser chance of returning to nest than females, males were replaced less often on a territory.

Breeding dispersal (Greenwood 1980) is the distance moved by an individual owl between its nest of one year (either the first or subsequent nestings) and the nest of the following year. Two categories of movements by flammulated owls between years were noted. The first category (3 cases) involved the same pair, or at least the same male of the pair, moving (\bar{x} = 71.7 m, SD = 44.2, range 30-118 m) to a different nest tree from one year to the next, but staying within an existing territory. Because these movements occurred within a territory, they were not considered breeding dispersal. The second category involved the changing of territories between years. This dispersal occurred only among females (5 of 10 that returned to nest) and averaged 474 m (SD = 201.8, range 256-798 m) (fig. 1). The mean dispersal distance was only slightly greater than the mean distance across the measured home ranges (424 m) (Linkhart et

al., in review). Thus, on average, females dispersed to adjacent territories. Harvey et al. (1979) found that great tits (*Parus major*) in England also dispersed the distance of a territory's width.

The proximate reasons for dispersal of females could not be determined; however, in all but one case, the original male at the abandoned territory had not returned. The exception involved a male (A12) who was unpaired for at least 1 year (1983) but who nested the following 2 years in the same territory but with different females (fig. 1). The original female (A29-83) had dispersed (798 m) to this territory in 1984, and the second female (A15-84) dispersed 495 m to the territory the following year (1985). There was no evidence that the first female (A29-83) returned to the study tract in 1985. Also, all but one dispersing female paired with an experienced male. In 1984, the male of A29-83 did not return and was replaced by an unbanded male (A29-84) who had paired with female A24-83 from an adjacent territory. The nest of A24 female had failed in 1983, and the fate of her original male was unknown. In only this case did a previously nesting female disperse to pair with a first-time nesting male--all other dispersals were to territories of males that had either nested, or were at least presumed to be the same male that defended a territory (e.g., A12), in previous years.

The nesting success of pairs (number of fledglings) may be related to the nesting experience of adults (table 3). Pairs consisting of males and females known to be nesting for the first time had an average of 0.58 fewer ($t = -2.02$, $df = 8$, $p < 0.1$) fledglings than pairs consisting of males and females known to have nested previously. If this relationship exists, there is a reproductive advantage for a male to return to its previous territory and for a female to choose an experienced male. We assumed that birds nesting for the first time on the tract were first-time breeders. The strength of our assumption obviously depends on the size of a study area and the likelihood that males in fact are not long-distance dispersers. However, because females are known to change territories, they may have dispersed onto the tract after nesting elsewhere. As a result, the category of first-time nesting females in the table may actually include experienced breeders. If so, any differences in brood size between experience categories would be diluted.

DISCUSSION

As in many other birds, flammulated owls demonstrated a marked between-year site fidelity, with males showing more faithfulness than females. The apparent absence of breeding dispersal in male flammulated owls may be related to the benefits accrued to males who establish territories in areas where they have had previous experience with the spatial and temporal variation in resources. Previous

Table 2.--The number of known replacement males and females on territories used more than once.

Territory	Males		Females	
	Replacement	Opportunities ¹	Replacement	Opportunities ¹
A24	0	2	0	2
A29	1	4	1 ²	4
A4	1	2	1 ²	2
A39	1	2	1	2
A15	1	2	1 ²	2
A12	0	3	2 ³	3
A11	0	2	1	2
MN1	0	1	0	1
Total	4	18	7	18

¹Opportunities is the number of years that a territory was reoccupied by any male or female. Tally was not limited to territories reoccupied in consecutive years.

²Involved a female changing territories between years.

³Involved two females changing territories between years.

Table 3.--Relationship between male and female nesting experience and productivity (number of fledglings). Three pairs that nested in 1986 are included.

	Number of fledglings			
	Males breeding 1st yr ¹		Males breeding > 2 yr ²	
	\bar{x} (SD)	n	\bar{x} (SD)	n
Females breeding 1st yr ¹	2.25 (0.50)	4	2.50 (0.71)	2
Females breeding > 2 yr ²	2.67 (0.58)	3	2.83 (0.41)	6
Combined	2.43 (0.53)	7	2.75 (0.46)	8

¹Males and females in the first yr are assumed to be first-time nesting birds (see text).

²Males and females nesting 2 or more yrs are birds known to have previous nesting experience.

experience may also predispose them to better establish and defend territories.

Because female flammulated owls are not involved in territorial defense and their role is primarily one of incubating and brooding (Reynolds and Linkhart this volume), they should pair with males already established in suitable habitat. If, upon return to their territory in the spring, their previous mate has not returned, females should immediately abandon that territory and pair with another male in suitable habitat. If nesting success is related to nesting experience, then a dispersing female should choose an experienced male with which to pair. If a female can recognize the voice of neighboring males from previous years, she could likely identify an experienced male in territories adjacent to her previous territory; that is, female breeding dispersal should be on the order of the width of 1-2 breeding territories. That females have the opportunity to judge the success of adjacent pairs is demonstrated by the occasional visits females made to the nests of adjacent pairs.

Species composition and structure of the forests on our study tract undergo relatively little change within the life span of individual flammulated owls. Site fidelity is expected to be prevalent among species living in stable environments (Harvey et al. 1979). Also, sexual differences in dispersal distances is likely to occur in species in which territorial establishment and defense is the duty of one sex and where success of the territorial defender is enhanced by retention of the same breeding area from year to year (Greenwood and Harvey 1976). In flammulated owls, it appears that competition among males for females is mediated through the ability of males to gain and hold a territory. Females do not have the costly constraint of establishing and defending territories. They do, however, have the option of choosing between available territories and/or males, provided they arrive on the nesting grounds early enough--that is, while there still are available

males.

Young males attempting to establish territories for the first time may be forced to occupy less suitable habitat and may remain unpaired until suitable habitat becomes available. In fact, we found unpaired, territorial males in small patches of old-growth ponderosa pine--Douglas-fir on the periphery and outside of our study tract. These males were difficult to capture and were not banded. Because of this, it was not known if the replacement males on our study tract were formerly peripheral males which had moved into vacated nesting territories. However, if young, inexperienced males occupied less suitable habitat for one or more seasons, this could account for the lower return of males compared to females--males may already be 2-3 years old before they gain breeding territories.

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The Nesting Biology of Flammulated Owls in Colorado¹

Richard T. Reynolds² and Brian D. Linkhart³

Abstract.--Spring arrival of flammulated owls to a 452-ha area in Colorado occurred in early May. Each year, 4-6 territories were occupied by pairs and 2-3 territories by unpaired males. Clutch size was 2.7 eggs, incubation was 22 nights, brood size was 2.4 young, and young were in the nest 23 nights. Owlets dispersed in late August and adults in early October. The affinity of flammulated owls for old yellow pine forests stems from the abundance of nest cavities, the structure of the trees and stands, and the arthropods found in these forests.

INTRODUCTION

The flammulated owl (*Otus flammeolus* [Kamp]) is a little known insectivorous species (Ross 1969) that is widely distributed in montane forests from southern British Columbia southward through the highlands of Mexico and Guatemala (Bent 1938). The owl is one of the smallest in this region (Earhart and Johnson 1970), is an obligate cavity-nester, and is assumed to be migratory in the northern part of its range (Marshall 1957, Winter 1974, Balda et al. 1975). It breeds from the Rocky Mountains (Reynolds and Linkhart 1984, and others) to the Pacific (Winter 1974) and from southern British Columbia (Cannings et al. 1978) south to Vera Cruz, Mexico (Sutton and Burleigh 1940). The winter range is thought to be from Guatemala and El Salvador north to Jalisco, Mexico (Phillips et al. 1942).

In spite of its wide distribution, little is known of the flammulated owl's nesting biology and population status. In fact, its status is so obscure that gross population changes would remain undetected.

Flammulated owls typically are found in the yellow pine belt--from lower elevations where the pine is mixed with oak (*Quercus* sp.) (Marshall 1957, Marcot and Hill 1980) or pinyon pine (*Pinus monophylla*) (Huey 1932) to its upper

reaches where the pine mixes with firs (*Abies* sp.), Douglas-fir (*Pseudotsuga menziesii*), larch (*Larix* sp.), or incense-cedar (*Libocedrus decurrens*) (Marshall 1939, Phillips et al. 1964, Johnson and Russell 1962, Bull and Anderson 1978, Reynolds and Linkhart 1984). The owl also has been recorded in quaking aspen (*Populus tremuloides*) (Webb 1982) and second-growth ponderosa pine (*P. ponderosa*) (Winter 1974). However, only Bull and Anderson (1978), Reynolds and Linkhart (1984), and Goggins (1986) extensively searched for nests, and only Reynolds and Linkhart (1984) estimated the density of nesting pairs. The owl's preference to forage in old-growth (> 200 yr old) ponderosa pine-Douglas-fir stands (Linkhart et al. in review)--a type and age class that is extensively managed in North America--its dependence on cavities for nests, and reports that the owl is not found in cutover forests (Marshall 1957, Phillips et al. 1964, Franzreb and Ohmart 1978) suggest a critical need for information about its nesting biology, nesting density, and habitat affinities.

We studied flammulated owls in the montane forest in central Colorado from 1980 to 1986 (Reynolds and Linkhart 1984, this volume; Linkhart and Reynolds, in press; Linkhart et al., in review). Nesting pairs and non-nesting territorial males on the study tract, as well as several pairs outside the tract, were studied each year. Movements and habitat use by nesting owls were determined with radio-telemetry in 1982-1983. Here we report the density of territorial males, territorial and nesting behavior, productivity, and foraging, and discuss the habitat associations of this owl.

STUDY AREA

The study was conducted on a 452-ha area of the Manitou Experimental Forest in central Colorado. Forest on the study tract consisted

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of open, park-like stands of ponderosa pine mixed with Douglas-fir on south- and west-facing slopes, dense stands of Douglas-fir mixed with blue spruce (*Picea pungens*) on north aspects, limber pine (*P. flexilis*) mixed with ponderosa pine and Douglas-fir on ridgetops, and quaking aspen mixed with blue spruce in drainage bottoms. Ages of the forest stands on the tract, as well as on the surrounding slopes, were mature (100-200 yr) to old-growth (200+ yr), but stands of second-growth (< 100 yr) occurred on most north-facing slopes.

Understories on slopes consisted of shrubs, such as common juniper (*Juniperus communis*), kinnikinnik (*Arctostaphylos uva-ursi*), cliffbush (*Jamesia americana*), and numerous grasses and forbs (Reynolds et al. 1985). Understories in creek bottoms consisted of willow (*Salix* spp.), water birch (*Betula occidentalis*), Rocky Mountain maple (*Acer glabrum*), grasses, and forbs. Elevations ranged from 2,550 to 2,855 m. The tract had not been logged since the 1880's, and snags (many containing suitable nesting cavities) were common on all slopes and aspects (Reynolds et al. 1985). Scattered snow drifts remained on the tract into early May, and a light to heavy snow fell 1-3 times per week through the month of May. Mean nightly low temperatures (taken in 1983) were -1.7° C for May, 2.8 for June, 7.3 for July, 7.9 for August, 2.2 for September, and -1.6 for October.

METHODS

Owls were observed from early May to mid-October, 1980-1985, and during 1 week in mid-July in 1986. Behavior was used to identify the sex of owls: males by their courtship feeding, copulatory and territorial behavior, and high level of activity during nesting; females by their recipient role in courtship feeding, food-begging vocalizations, and low level of activity during nesting (Reynolds and Linkhart 1984, Linkhart et al. in review). The sex of owlets was not determined.

Breeding adults were located from early May to late July by imitating their territorial song (Marshall 1939, Winter 1971, Marcot and Hill 1980). Prior to egg-laying, adults were located by their courtship vocalizations. Territory boundaries were identified by marking the song trees of singing males (after Wiens 1969). Once territory boundaries were known, all tree cavities with entrance diameters greater than 4 cm were checked for nesting owls (Reynolds and Linkhart 1984). Incubation period was the time (nights) from laying to hatching of the last egg. Fledged young were located by their food-begging vocalization, calls of attendant adults, and radio-tagged individuals (Reynolds and Linkhart 1984, Linkhart et al. in review).

Radio-telemetry was used to determine home range size, foraging locations, and activity of owls in 1982-1983 (Linkhart et al. in review). Capture of owls is described by Reynolds and

Linkhart (1984). Males were equipped with tail-mounted or backpack-mounted transmitters (3.0 g) shortly after egg-laying, and females and young were equipped with backpack-mounted transmitters (Reynolds and Linkhart 1984). We followed the radio-tagged owls with a portable radio-receiver and hand-held yagi antenna.

Composition of diets and frequency of food delivery were determined by observing males delivering food to females during courtship and later to nests. Observations at nests were facilitated by gasoline lanterns, binoculars, and cameras placed adjacent to nest cavities (Reynolds and Linkhart 1984).

Foraging behavior was determined by observing radio-tagged owls and incidental observations of nonradioed owls. The rate of food delivery during courtship, incubation, and nestling stages was determined during 61 observation bouts (total 97 hr) between 20:30-03:00 hr MDT from 1981-1984 (16 hr during courtship for 9 pairs, 26 hr during incubation at 8 nests, and 55 hr during the nestling stage at 12 nests). Mean length of observation bouts was 1.6 hr (SD = 0.90, range = 0.5-3.9). Hourly delivery rates were calculated by dividing the total number of deliveries tallied per hour per night at nests by total hours of observation at nests. Hourly rates were grouped in 4-night intervals, and a mean hourly rate among the 4 nights was calculated. This procedure was used to determine the delivery rates during courtship and incubation stages.

Because females were fed in the cavities for only the first 12 nights of the nestling stage, and brood size varied among nests (2-3 nestlings), the delivery rate during the nestling stage could not be determined directly. To estimate the rate after hatching, we first assumed that females consume two arthropods per hour during the 12 days after hatch (the delivery rate during the last days of incubation). We then subtracted two deliveries per hour per female from the total deliveries tallied during a night's observations. The remaining number of deliveries then was divided by the number of young being fed, and a mean hourly rate per young for each 4-night period was determined as above. A delivery rate for a brood of three was estimated by multiplying the mean hourly rate per young by 3.

Body mass of adults and owlets were determined to the nearest 0.5 g with Pesola spring scales. No attempt was made to adjust for stomach contents. Adults were weighed at night after some foraging had occurred. Nestlings were weighed in the latter half of the diurnal fasting period. We examined seasonal lability of body mass using mean weights of owls captured during the stages of nesting. Seasonal changes in mass of individuals, for which we had repeated measures, mimicked the seasonal patterns of the means.

Nocturnal flying insects on the study tract were sampled during the summer of 1981 and 1982 using a battery-powered (12-volt) black-light trap fitted with a photo-sensitive cell. The trap was operated at a lower-slope position for 1 to 3 nights/week from 20 May-27 August 1981 and 1-2 nights/week between 18 May and 29 September 1982. Traps were cleaned each morning. Specimens of each species were pinned, and the number of individuals per family per night counted.

In the summer of 1980, we placed 17 nest boxes (see Gary and Morris 1980 for dimensions) within the home ranges of six males. Boxes were placed below the crowns on trunks of large-diameter trees (all between 3-4 m high).

RESULTS

Spring Arrival, Pair Formation, and Territoriality

Some adult males appeared on territories as early as the first week of May, and all territories were occupied by the third week of May. Although some females arrived in early May, they appeared to arrive over a longer period than males. A few owls, apparently already paired, were observed as early as 3 May at nests used in previous years. Nesting males sang frequently during the incubation period, but less often after the eggs hatched. Territorial males that remained unpaired sang throughout the summer.



Foraging habitat of Flammulated Owls on the Manitou Experimental Forest.

During the courtship period, pairs moved through their territories visiting prospective nest-cavities. Males entered cavities and gave quiet, hoarse "boop-boop" calls once inside. Females followed males into cavities. After a nest tree had been selected (usually by late May), females remained in the close vicinity of the tree. During courtship feeding, males approached females and gave quiet "boop-boop" calls to which females responded with food-begging ("meow") vocalizations. Males then perched next to females and transferred food to them. Copulation, when it occurred, usually followed food transfers. On several occasions, the birds preened one another after copulating.

Each year, four to six nesting territories and two to three non-nesting territories were occupied on the tract (0.9-1.3 nests/100 ha and a maximum of 2 territorial males/100 ha). Counts of singing males in other areas ranged from 1 to 5 males per 40 ha (Marshall 1939, Winter 1974, Balda 1977, Franzreb and Ohmart 1978). Five territories were on the south-facing slope of the principal ridge running east to west through the tract, and during the years from 1981 to 1985, each of these five territories was occupied by pairs a mean of 3.0 yr (SD = 1.22, range = 2-5) (Reynolds and Linkhart, this volume). This south-facing slope had a continuous cover of old-growth ponderosa pine mixed with Douglas-fir. Two nesting territories in the northwest quarter of the tract contained a mosaic of stands of old-growth ponderosa pine--Douglas-fir, mature quaking aspen--blue spruce, and mature quaking aspen. One of these territories (A10) was occupied for a single year, and the other (A11) was occupied for 3 years (1983-1985) by the same male.

Two nesting territories were located in old-growth ponderosa pine--Douglas-fir on the upper portions of west-facing slopes of terminal ridges along the southern boundary of the tract. The area of old-growth in each was restricted; both territories were bounded below by young stands of Douglas-fir mixed with blue spruce. One of these territories (A18) was occupied by a nesting pair in 1981 and 1984 and an unpaired male in other years. The other territory (A12) was occupied by a courting pair in late spring of 1981. Although their nest was not located, the pair probably produced a clutch. In 1982 and 1983, this territory was occupied by an unpaired male. In 1984-1986, a male occupying this territory nested in trees in a creek bottom in the extreme northwest portion of his range. Observations of the male showed that he departed and arrived at the nest with food from the center of his territory on top of the ridge. In 1982, another pair nested on the periphery of a territory that had been occupied in 1980 and 1981 by an unpaired male. This pair (A10) nested in a quaking aspen in a creek bottom in the extreme southeast portion of the territory. The radio-tagged male primarily foraged 400 m to the northwest of the nest in old-growth ponderosa pine--Douglas-fir.

Observations indicate that males may expand their territories when adjacent territories are not occupied. Territory A24 contained a nesting pair during 1981-1983. In 1984 and 1985, A24 was not occupied, and a banded male from an adjacent territory (A29) day-roosted in the nest area of A24 during late summer and fall of both years (see fig 1, Reynolds and Linkhart, this volume). In 1982, territory A15 was occupied by a radio-tagged male who used the northern part of unoccupied territory A39. In 1983, a radio-tagged male in territory A4 used the eastern parts of unoccupied territories A39 and A15. Territory A39 was occupied in 1985 and 1986 while A4 and A15 were not. In 1986, the male in A39 nested 150 m to the east of his 1985 nest in a tree adjacent to the western-most nest of A4. In no year were all three of these territories occupied simultaneously.

In the 6 years (1981-1986) that nest boxes were available on our study tract, 2 of the 17 were used; a pair in territory A4 produced two fledglings in 1983 and a pair in A39 produced three fledglings in 1985. Use of nest boxes by flammulated owls in other areas has been reported (Hasenyager et al. 1979, Cannings 1982, Bloom 1983).

Nesting Chronology and Productivity

Mean clutch size for 11 pairs from 1981-1985 was 2.7 eggs ($SD = 0.47$, range = 2-3, mode = 3). The interval between laying of the first and second eggs was undetermined, but two nights elapsed between laying of the second and third eggs for two females. The mean date of clutch completion (the laying of the last egg) for 14 females was 7 June ($SD = 4.6$, range = 29 May-14 June). Observations at one nest indicate that incubation began after the second egg was laid. At this nest, two eggs were on opposite sides of the nest cavity on 8 June 1982 and the female was day-roosting on the floor of the cavity. On 9 June, the female sat tightly on the eggs, which had been moved to the center of the cavity. The clutch contained three eggs on the night of 10 June, and all eggs were touching one another.

The incubation period, determined for three clutches whose laying and hatching dates were known, was 22 nights ($SD = 0.6$, range = 21-22). All clutches hatched over two nights. The mean date on which the last egg hatched in 14 clutches was 29 June ($SD = 4.6$, range = 20 June-6 July). Mean size of 26 broods was 2.4 young ($SD = 0.80$, range = 1-3), and for 23 successful nests the mean number of fledglings per nest was 2.6 ($SD = 0.59$, range = 1-3). Mean length of the nestling period, determined for five broods, was 23 nights ($SD = 1.1$, range = 22-24), and mean fledging date for 14 broods was 22 July ($SD = 4.5$, range = 13-29 July). Broods fledged over two nights, and all broods separated shortly after fledging, with one portion of the brood being tended by the male and the other by the female (Linkhart and Reynolds, in press).

Owlets were foraging successfully and no longer provisioned with food by late August, 25-32 nights after fledging.

Sex Roles, Food, and Foraging

As in other strigiforms, there is a division of labor between the sexes in flammulated owls. Females were fed by males for 2 to 3 weeks (beginning as early as 23 May) prior to egg laying. Although we did not determine exactly when females ceased foraging, we never observed them doing so after courtship feeding began. In the few nights prior to laying, females spent the entire night perched within 20 m of the nest-cavity and were fed at high rates by males. Female body mass increased by as much as 68% before laying (see below). Females did all of the incubating and brooding. On the tenth or eleventh night after hatch, females began foraging and, through the remainder of the nestling stage, gradually increased the number of foraging trips. At the time of fledging, females had resumed foraging full-time.

Flammulated owls were entirely insectivorous (also see Ross 1969); most food items delivered to nests or fledglings were small- to medium-sized moths (mostly Noctuidae). However, by midsummer, the owls also captured various lepidopteran larvae, orthopterans, coleopterans, spiders, and other arthropods. When adults delivered food to nests or fledged young, they always brought one prey at a time.

Adults used four foraging tactics: hawk-gleaning, hover-gleaning, hawking, and drop-pouncing. Hawk-gleaning, which occurred inside the crowns of trees, consisted of flying from a perch inside the crown to take resting arthropods from branches, trunks, or inner portions of needle bunches. Hover-gleaning consisted of an owl flying from a perch in one tree to glean moths from the outer needles of adjacent crowns while hovering. Both hawk-gleaning and hover-gleaning, the most frequently used tactics, occurred in the more open lower two-thirds of tree crowns. From the middle of summer, and especially in late summer, adults and fledglings frequently dropped from the lower portions of a tree crown to pounce on arthropods on the ground, grasses, or shrubs. Hawking, the least frequently used tactic, occurred either within crowns or in the spaces between crowns and consisted of an owl leaving a perch to capture a flying insect and returning to a new perch.

Individuals of the lepidopteran family Noctuidae were by far the most abundant moths in the black-light trap samples during May-September (fig. 1). These moths never contributed less than 67% of the total catch in any month during the sample periods in 1981 and 1982. Only two other families, Sphingidae and Geometridae, were common in the samples; sphingids in the spring and early summer (a high of 18% in May) and geometrids in August (high of



The male Flammulated Owl always delivered a single prey item at a time to the nest.

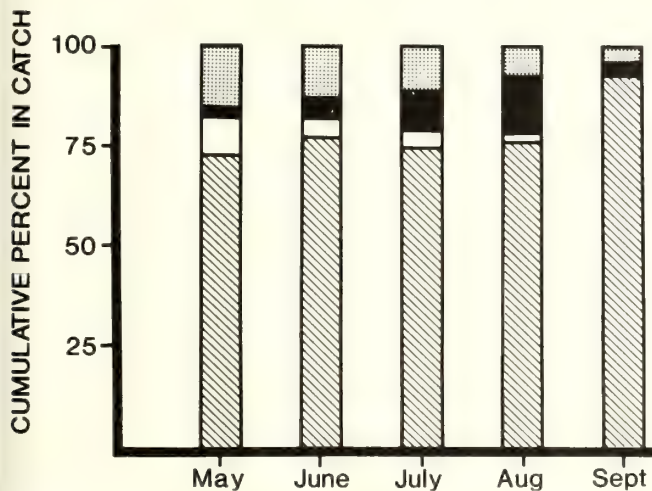


Figure 1.--Percent composition of lepidopteran (moth) families in black-light trap. Data are percentages of combined (1981 and 1982) catch by month. Striped bars = Noctuidae, open = Sphingidae, dark = Geometridae, stippled = all their families (Arctiidae, Saturniidae, Notodontidae, Lasiocampidae, Lithosciidae, Ethmiidae, Pyralidae, Tortricidae, Limnophiliidae). Total combined catch for May = 472 moths, June = 2,710, July = 4,973, August = 1,970, September = 203.

17%). Members of "all other families" were abundant in May, but their combined relative frequency declined as summer progressed. On our study tract, noctuids appeared to be the only food available to the owls during cold spring nights. These moths generally are robust, nocturnal insects with strong flight capabilities and were frequently seen in May flying about the forest canopy when temperatures were below freezing.

Seven nesting home ranges averaged 14.1 ha. Although owls foraged throughout these ranges, each range had 1 to 4 areas within which foraging by males was concentrated; 81% of 221 observed foraging attempts occurred in these intensive foraging areas (IFAs) (Linkhart et al., in review). Mean total area in IFAs within ranges was 1.0 ha (range = 0.6-1.5), and all but 1 of the 7 nests were contained within an IFA. Mean distance from nests to IFA centers was 125 m (range = 10-410). Of the 15 IFAs, 12 contained old-growth ponderosa pine--Douglas-fir, 2 contained mature quaking aspen--blue spruce, and 1 a mix of old-growth ponderosa pine--Douglas-fir and mature aspen. Although the behavior was not quantified, we observed males foraging in IFAs nearest their nests during bursts of foraging activity in the early evenings (see below) and at other times when food demands at nests were high. Males foraged

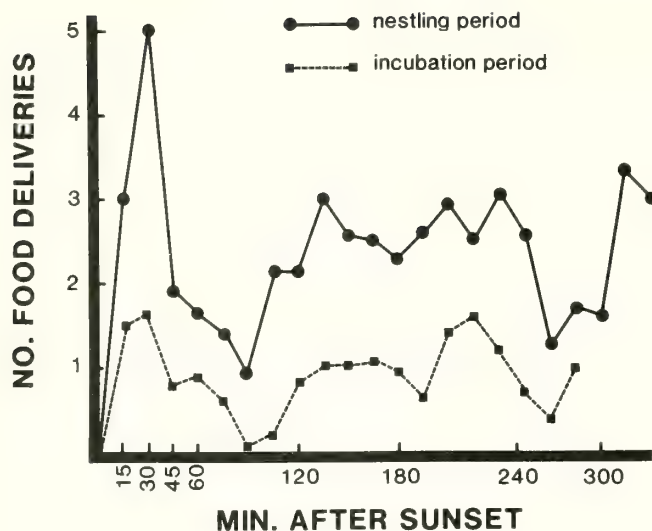


Figure 2.--The number of food deliveries to nests in 15-min. periods during incubation and nestling stages. Observations began at 20:30 hr and ended at 03:00 hr MDT, and were made at 8 nests (total 26 hr) during incubation and at 12 nests (total 55 hr) during the nestling stage.

in more distant IFAs when rates of food delivery to nests were low.

The pattern of nightly food deliveries by males during courtship and nesting was a burst of feeding activity 15-30 min after sunset, followed by a decline over the next hour, and then a return to an intermediate level for the remainder of the observation period (fig. 2). Observations at nests terminated at 03:00 hr, but radio-tracking of foraging males showed that the delivery rate continued at the intermediate level through the late night, and that another burst of food deliveries took place 1-1.5 hr before sunrise. Males stopped foraging and went to roost about 0.5 hr before sunrise. This pattern of food delivery was essentially the same at all stages of the nesting cycle, the only difference being the rate. A similar pattern was found for a single pair of flammulated owls in Idaho from hatching through the first two-thirds of the nestling period (Hayward 1986).

Nightly delivery rates from courtship through the nestling stages (fig. 3) show patterns associated with expected energy demands at each stage of the cycle. From the beginning of courtship feeding, males increased the rate of feeding of females to almost 12 moths per hr in the 4 days prior to laying the first egg--an increase associated with the energy demands of egg formation. After laying, food deliveries decreased to a low of about two moths per hour the 8 days prior to hatching. After hatching, the delivery rate increased and peaked at over 16 trips/hr during the period 8-12 days after hatch. It was at the end of this period that females began foraging. The subsequent decrease

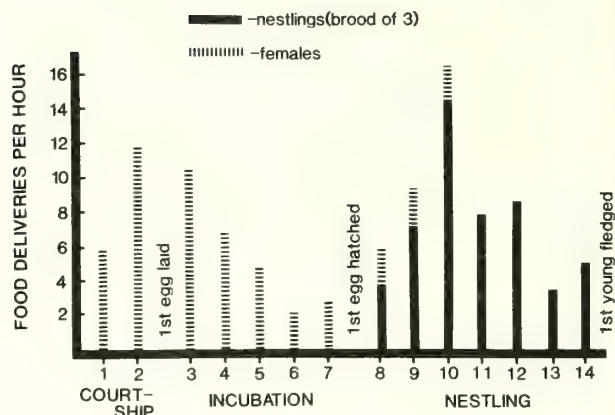


Figure 3.--Food delivery rates by males to females during courtship and to nests during incubation and nestling stages for 14 pairs of flammulated owls. Rate during the nestling stage represents the feeding of a brood of three young plus the female during the first 12 days and thereafter just the brood (see text). Mean observation period was 1.6 hr ($s = 0.90$, range = 0.5-3.9, $n = 61$), and all observation periods were between 20:30-03:00 hr MDT. Data are presented in 4-night periods, except for the last period in the incubation and nestling stages, which include 5 nights.

in deliveries probably reflects the decreasing growth rate of the young.

Adult owls ceased all activity during periods of snow or rain. For example, a severe thunderstorm at 22:00 hr on 25 June 1982 caused male A24 to cease foraging and seek shelter in a densely crowned ponderosa pine. As the storm intensified, the male changed trees three times, apparently seeking better shelter. Inclement weather also caused fledglings to become inactive. During 5 consecutive nights (25-29 July) of rain, the adults in A10 fed the owlets infrequently and only during periods of light rain, despite the frequent food-begging of the young. The fledglings perched near the ground on rocks, logs, and stumps during the rain.

Changes in Body Mass During Nesting

Body mass of adult females varied considerably through the nesting cycle (table 1). Female mass peaked just before egg laying. Female A10-82 was 96.0 g five nights prior to laying her third egg--39.0 g heavier than two nights prior to the fledging of her brood. During capture attempts on the night before egg-laying, females flew with difficulty and, after several flushes, ended up perched low to or on the ground. Females gradually lost weight after egg-laying. Female A11-83 was 68.0 g the night after her eggs hatched, 7.0 g less than she weighed 13 nights prior to laying. Mean mass of 16 adult females during the nestling stage was

Table 1.--Body mass of adult flammulated owls in four stages of the nesting cycle. Body mass of owls weighed more than once in a stage were averaged.

Stage	Males			Females		
	$\bar{x}(n)$	SD	Range	$\bar{x}(n)$	SD	Range
Prelaying				81.7(3)	12.42	74.0-96.0
Incubation	56.7(9)	3.42	53.0-62.0	78.3(4)	7.92	76.5-85.5
Nestling	53.2(15)	2.09	49.5-56.5	63.3(16)	4.45	56.0-70.5
Fledgling	55.8(3)	7.07	50.0-60.0	58.2(2)	6.72	53.5-63.0
Total season	54.7(27)	3.28	49.5-62.0	65.6(25)	10.85	53.5-96.0

63.3 g, a decrease from a mean of 78.3 g for four females during the incubation stage ($t = 5.17$, $df = 18$, $p < 0.05$).

Body mass of males fluctuated relatively little through the cycle (Table 1). The mean mass of nine males during incubation was 56.7 g. After hatching, the mean mass of 15 males was 53.2 g ($t = 3.13$, $df = 22$, $p < 0.05$). One male (A4-83) was 56.0 g three nights prior to hatching; 58.5 g three nights prior to fledging; and 60.0 g eleven nights after his young fledged. Two nights after his brood subgroup achieved independence, the male had dropped to 56.5 g. In mid-September (24 days post-fledging), he still was 56.5 g. However, on 6 October, the male was 67.0 g--a gain of 10.5 g during the previous 3 weeks. The male, radio-tagged, left the study tract on the night of 12 October.

Loss of weight by females after hatching to a low during the molt in September was similar to weight changes of nesting female long-eared owls in the Netherlands (Wijnandts 1984). Weight decrease of male flammulated owls, however, was not as great as the 12% decrease among male long-eared owls during nesting.

Owlets were first weighed 6-10 days after hatch (fig. 4). Mean mass of 11 nestlings was 61.3 g during the 5 days prior to fledging. In the 5 days following fledging, mass decreased to a mean of 54.6 g and ranged from 38.0 to 68.0 g. Some weight loss may have resulted from the increased activity associated with free flight, but most is attributable to decreased feeding during inclement weather that occurred at the time of fledging each year. For example, one owlet was 48.0 g 6 days prior to fledging, 44.0 g 2 days after fledging (26 July), and 38.0 g 5 days after fledging (29 July). Two siblings of this owlet also lost weight during this period--one was 56.0 g at fledging and 48.0 g 6 nights after fledging, and the other 51.0 g 5 nights before fledging and 50.0 g 5 nights after fledging. Weather on these 5 nights consisted of late afternoon or evening thundershowers followed by late night tree drip and fog. These and other owlets gained weight through the next 10 days, when, after independence, they again lost weight.

Predation and Mortality

There was no evidence of predation on adults or nestlings during the study. However, many old nesting cavities in quaking aspen on the study tract had been broken open by black bears (*Ursus americanus*). Predation on a flammulated owl nest in Colorado, by either a bobcat (*Lynx rufus*) or black bear, was reported by Richmond et al. (1980).

Three radio-tagged fledglings in our study were killed by predators within 6 days after fledging. Two were killed by *Accipiter* sp. and the third by an unknown mammal. Only one adult death was noted. A female (A11) was begging for food approximately 300 m west of her nest on 2 August 1983, 2 nights after her young fledged

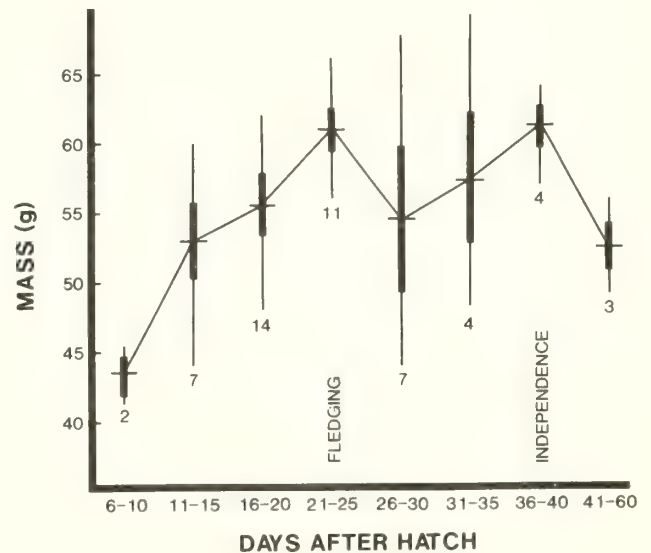


Figure 4.--Changes in body mass of owlets from 6-10 days after hatching. Horizontal bars are mean weights, thick vertical bars are 1 standard deviation around means, and vertical lines are ranges. Numbers below bars are number of owlets weighed during period.

and 1 or 2 nights after one of the fledglings was killed. Two males, one probably her mate, appeared to be feeding her, but she also captured several moths. She weighed 60 g and was well into the molt of her primaries. We attached a transmitter, and on 3, 4, and 5 August, she was observed on day-roosts. However, she was found dead 2 km from her nest on 8 August, and the emaciated carcass weighed 40.0 g. We had not observed other females begging for food after their broods had fledged.

Molt

Although all owls were examined for molt with each capture, only 5 adults were captured while molting. The molt of one male was assessed four times (4 and 19 August, 13 September, and 6 October) and once each for two other males (23 July and 18 September). Two females were assessed once each (18 July and 2 August). These assessments indicated that molt of the primaries in males and females is sequential (1 through 10), beginning during the second or third week of July and, at least for males, is completed by the end of September. Molt of the secondaries began in late September for one male, and there was no apparent order to the loss of secondaries. Tail molt in both males and females began with the central rectrices in early August and appeared to be centrifugal (Mayr and Mayr 1954). However, because only a few rectrices had been lost by October in birds assessed, the tail molt may be partial in this species (see Forsman 1981). We saw no evidence among owls observed or captured that molt of the rectrices was simultaneous (*contra* Bloom 1983).

Owlets were sparsely covered by white natal down after hatching. Within 10 days after hatch, a soft gray and horizontally banded juvenal plumage began to replace the natal down. The juvenal plumage was nearly completed at fledging, and the remiges of the owlets were about three-fifths and the rectrices about one-half developed. Both remiges and rectrices reached full development between 20 and 25 days after fledging. Replacement of the juvenal plumage began around the eyes several days after fledging and progressed slowly through the end of August. When owlets left our study area in late August, they retained some juvenal plumage on their backs and lower undersides.

DISCUSSION

Flammulated owls delivered prey to the nest at a greater rate during the first hr after dark and irregularly thereafter whenever food demands at nests were high. Males minimized travel time by foraging in IFAs close to the nest during these periods. Foraging in distant areas between periods of high demands may (1) reserve food in near patches, (2) reduce the attraction of predators to the nest, (3) facilitate territorial defense, or (4) allow more varied prey to be captured (Brooke 1981, Tinbergen 1981, Kacelnik 1984). Even though foraging in distant

patches increased the travel time, the effect was minimal because distant foraging occurred when food demands were low. It is interesting that the flammulated owl does not deliver more than a single food item per foraging trip. For birds feeding on prey whose mass seldom exceeds 0.5% of their mass, the high feeding rate at nests is not surprising. Furthermore, because the male is the sole provider of food through much of the nesting cycle, it is not surprising that most nests were contained within an IFA.

Linkhart et al. (in review) report that returning flammulated owls settled in stands of old-growth (> 200 yr) ponderosa pine--Douglas-fir and avoided other overstory types. Furthermore, after settling, the owls significantly preferred to forage in old-growth pine--fir patches and avoided young (< 100 yr), denser stands of Douglas-fir mixed with blue spruce. Other studies of this owl (e.g., Marshall 1939, 1957; Johnson and Russell 1962; Cannings et al. 1978; Bull and Anderson 1978; Winter 1974; Marcot and Hill 1980; Goggins 1986) associated the bird with mature trees of one of the yellow pines [Subsection *Ponderosae* (Laud.)] (Critchfield and Little 1966) mixed with other conifers or hardwoods.

The reasons for this association likely involves both food and habitat. First, the owl is an obligate cavity-nester, and older forests typically have an abundance of snags and live trees with suitable cavities. Second, old yellow pines typically form open stands with extensive grass or shrub understories (Moir 1966, Franklin and Dryness 1969). The understories provide a substrate for feeding and resting arthropods, and drop-pouncing to this substrate was frequently used by the owls during late summer (this study, Goggins 1986). Third, because widely spaced trees allow for greater movement of air, and therefore, faster drying and warming (Sukachev and Dylis 1964), moisture (within-canopy drip) from rains evaporate faster in open-canopied forests. As a result, the activity of arthropods--and foraging by the owls--would resume sooner in open forests after a rain. Fourth, although the abundances of noctuids and other arthropods, and the extent to which they are limited to pine-fir forests are unknown, many are host-plant specific and tend to be limited to specific habitats (Munroe 1979). Also, there are up to 4-times as many lepidopteran species associated with ponderosa pine or Douglas-fir than with other common western conifers (Furniss and Carolin 1977). Before the role of food in the owl's choice of habitat can be assessed, however, the composition, abundance, and activity periods of arthropods in the western forest types must be determined. Finally, at least 3 foraging tactics (hawk-gleaning, hover-gleaning, and hawking) require large, open crowns, and space between crowns. The interior portions of the crowns of large yellow pines and associated conifers (e.g., Douglas-fir) are open, exposing limbs and trunks that provide the owls with

perches and access to areas where arthropods rest. The openness of these stands also provides space between trees for hawking and gleanng insects. That the unique structure of older ponderosa and jeffrey pine (*P. jeffreyi*) forests in the north of the owl's range also occurs in similar yellow pine forests in their winter range (Mexico and Central America) suggests that the owl's foraging repertoire could be fine-tuned to this structure and, perhaps, to associated arthropods.

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STUDY AREA

Surveys were conducted along the South Thompson River drainage within an area approximately 70 km long and 20 km wide near Kamloops, British Columbia (Fig. 1). The area is an incised valley within the intermontane Thompson Plateau where maximum elevations approximate 2000 metres. Elevations within surveyed areas ranged from 350–1300 m. The forests in the study area consisted of ponderosa pine at lower elevations and mixed Douglas fir – ponderosa pine at middle elevations and south-facing slopes. Above 850 m, Douglas fir was dominant and ponderosa pine occurred as a seral species after fires and persisted as a veteran subdominant on drier, south-facing slopes. Trembling aspen occurred as a seral species on wetter ecosystems. At the highest elevation, Douglas fir maintained its dominance but lodgepole pine (*Pinus contorta*) occurred as a seral or fire climax species on drier sites. Selective logging had occurred extensively throughout the study area for at least 100 years resulting in mixed age stands and variable tree densities. Old growth stands (200+ years) generally occurred only on sites unsuitable for timber harvesting. Elsewhere, stand age classes ranged from mature (100–200 years) to second growth (< 100 years). Within most age classes, selective harvesting had resulted in variable canopy closures and stand structures. Snags and cavity-bearing trees occurred in varying densities throughout the area. The forest understory depended upon stand history, canopy closure and topographic factors but generally consisted of mixtures of grasses, forbs and shrubs as described by various authors (Mitchell and Green 1981, Brayshaw 1965, Tisdale and Maclean 1957). Common species were bluebunch wheatgrass (*Agropyron spicatum*), pinegrass (*Calamagrostis rubescens*), birch-leaved spirea (*Spirea betulifolia*) and saskatoon (*Amelanchier alnifolia*). Terrain was moderately steep (25–75 per cent slope.). Annual precipitation averages 32–43 cm with annual maxima in May–June and December–January. The mean annual temperature is -4 to -6°C with a mean July temperature of approximately 16°C . (Mitchell and Green 1981). With increased elevation, precipitation increases and temperatures decrease in the study area. More frequent surveys were conducted on Wheeler Mountain within the Tranquille Provincial Forest. The forest type was predominantly Douglas fir with ponderosa pine occurring on some south-facing slopes. The area was selectively logged 20–30 years prior to the surveys but many old and mature trees still existed. Stand ages varied from 80–200+ years with complexity provided by second-growth firs. Thickets of regenerating firs were common as were openings up to 1 or 2 ha in size. The forest structure was generally open but quantitative measurements were not made.

METHODS

Literature records and information from observers were obtained for areas throughout British Columbia where Flammulated Owls had been observed. From 1979–1986, random site visits were made to locations near Kamloops where owls were expected or known to occur. Birds were located by listening for singing males or eliciting responses by playing tape recorded territorial songs during May, June and early July. From 1983–1985, 10 linear census routes were driven along roads penetrating forests within the ponderosa pine and Douglas fir forest belts. The routes were driven between 2200 and 0100 hours during May, June and early July and stops were made every 0.5 km. Routes varied from 3–10 km in length. At each stop the first three minutes were spent listening for singing birds. If none were heard, a tape recorded song was played in order to elicit responses. The locations of all birds were plotted as closely as possible on 1:50,000 scale topographic maps. Weather conditions were noted and generally, routes were not surveyed during rain or if wind noise was considered excessive.

Given the terrain, forest cover and other factors, it was assumed that the radius within which owls might be heard would not exceed 0.5 km. Across open grasslands under very quiet conditions, birds have been heard up to 0.75 km away but this was considered exceptional.

An approximation of the area in hectares surveyed aurally (soundscape) along each route was calculated using the formula:

$$100 [n(.78) - (n-1).24]$$

where n equals the number of stops per route. This overestimates the actual area censused due to the curvilinear nature of the outer boundaries of the soundscape. Density figures were converted to singing males per 40 ha. Habitat characteristics were derived from simple field observations and forest cover maps prepared by the British Columbia Ministry of Forests and Lands. Detailed field measurements of tree and stand characteristics were not made.

RESULTS

DISTRIBUTION

Literature evidence and surveys resulted in records for 104 Flammulated Owls between 1902 and 1986 (Table 1). This included 10 juvenile, recently-fledged or nestling birds. Three centres of abundance are shown in Figure 2: the Okanagan Valley, the South Thompson River Valley and the southern Rocky Mountain Trench. The most northerly records occurred near Kamloops at $50^{\circ} 51'$ latitude and at Radium in the Rocky Mountain Trench at $50^{\circ} 40'$ latitude. Near Kamloops birds were recorded

west to 120° 55' longitude and east to 119° 50'. In the Okanagan Valley, records were obtained for the Vernon, Kelowna, Penticton and Okanagan Falls area south to about 40° 15' latitude. The Okanagan Valley runs generally north-south such that all sightings were between 119° 15' and 119° 35' W longitude. In the Rocky Mountain Trench all records were from the Radium-Windermere area at 50° 40' N latitude. Throughout the province, owls were only recorded between 375 m and 1250 m in elevation. Records occurred from 4 May - 22 October but the latest that a live bird was seen was 14 September. The 22 October record was of a dead bird and was an estimate of time of death (Brooks 1909).

HABITAT SELECTION

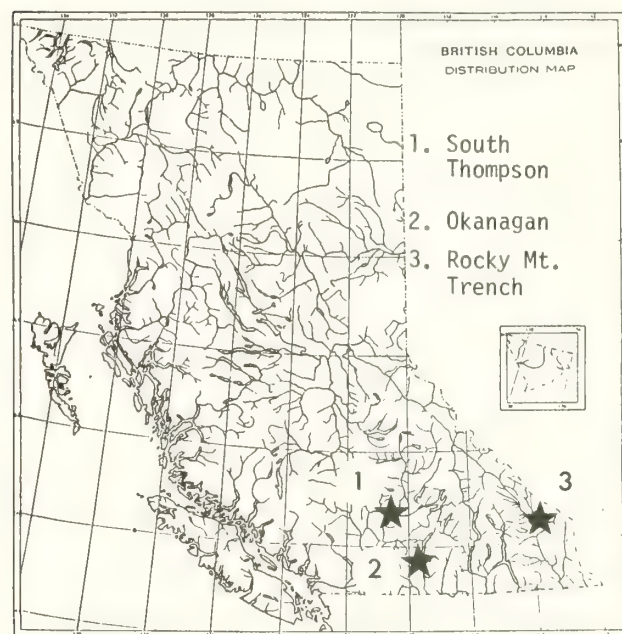
Except for 3 occasions, all birds were found within the interior Douglas fir biogeoclimatic zone (Krajina 1969). Within the more intensely surveyed study area near Kamloops, birds were

Table 1.--Summary of Flammulated Owl Sightings in British Columbia 1902-1986.

Year	# Birds	General Location	Reference
1902	1	Penticton	Brooks, A. 1909
1935	1	Kamloops	Williams & Spencer, 1942
1947	1	Penticton	Cannings, S.(pers. comm.)
1962	1	Penticton	Atkinson, R. 1963
1975	1	Radium	¹ Van Tighem, K. 1977
1977	1	Windermere	B.C.P.M.
1977	4	Penticton	Cannings, R.J. et al. 1978
1978	2	Penticton	B.C.P.M.
1979	3	Penticton	B.C.P.M.
1979	2	Kamloops	B.C.P.M.
1979	2	Kamloops	Howie, R. (unpub. rep.)
1980	2	Okanagan Falls	B.C.P.M.
1980	4	Penticton	Cannings & Cannings 1982
1981	2	Penticton	Cannings & Cannings 1982
1981	5	Kamloops	Howie, R. (unpub. rep.)
1982	2	Kamloops	Howie, R. (unpub. rep.)
1983	11	Kamloops	Howie & Ritcey (unpub. rep.)
1983	2	Penticton	B.C.P.M.
1984	19	Kamloops	Howie & Ritcey (unpub. rep.)
1984	2	Pritchard	Bowling, J. (pers. comm.)
1984	3	Kelowna	Bowling, J. (pers. comm.)
1984	1	Vaseaux Lake	Cannings, R.J. (pers. comm.)
1985	21	Kamloops	Howie & Ritcey (unpub. rep.)
1985	1	Vaseaux Lake	Cannings, R.J. (pers. comm.)
1986	7	Kamloops	Howie, R. (unpub. rep.)
1986	5	Penticton	Cannings, S. (pers. comm.)

¹ British Columbia Provincial Museum Sight Records File.

Fig. 2-- Flammulated Owl Centres of Abundance



confined to a drier subzone referred to as the "very dry submontane interior Douglas fir (IDFa) (Mitchell and Green 1981). Observations of the habitat elsewhere in the province where Flammulated Owls have been recorded confirm a strong association with this forest type. No birds were found in the ponderosa pine belt. Near Kamloops where 70 per cent of all sightings have occurred, some owls were found in old growth (200 + yr) Douglas fir with veteran ponderosa pines scattered throughout the area. One site was moderately steep (60 per cent), south facing and had been selectively harvested more than 50 years prior to our survey. Most owls were found in mature-old (100-200 yr) growth stands of Douglas fir that had been selectively harvested 20-30 years prior to our surveys. On the intensively surveyed Wheeler Mountain (50° 46' N, 120° 28' W) stand age classifications ranged from 80-240 years with most of the area in the 140-250 year class. Harvesting had removed many large stems but veteran Douglas fir and ponderosa pine were common. The forest structure was generally open with canopy closure ranging from 35-65 per cent except in thickets of regenerating Douglas fir. At least two canopy layers were present in areas where owls were found with older firs and pines forming the upper layers and second-growth firs forming the lower layers. A poorly-developed shrub layer was generally present and was dominated by Saskatoon. Depending upon site moisture and canopy characteristics, the herb layer was well-developed and consisted of Pinegrass or Bluebunch Wheatgrass and various sub-dominants. Birch-leaved Spirea occurred on many sites.

No owls were found in clearcut areas nor areas where the general age class of the forest was less than 80 years. One bird was found in

mature timber adjacent to a regenerating clearcut and one bird was calling from a copse of Trembling Aspen in grassland but older Douglas fir forest was present within 250 m.

Densities

Survey results from 10 census routes near Kamloops are given in Table 2. Considering the soundscape censused along the entire length of the routes, densities of singing males ranged from .03 - .5 per 40 ha on surveys where birds were heard. On all except the Wheeler Mountain route, the number of males heard per survey ranged from 0-3. Distribution of males along the Wheeler Mountain route was not consistent between years and appears to be clumped (Table 3). Considering only the soundscape censused between the first and last stops where owls were heard, density estimates were higher than for the entire route and varied from 0.4 - 0.7 singing males per 40 ha. (Table 4). On two sites on Wheeler Mountain, more intensive ground surveys located 3 and 4 singing males within two 100 ha areas or 1.2 - 1.6 males per 40 ha. On a third site on Mount Fleet, 2 males were singing within an 80 hectare area or 1 bird per 40 ha.

DISCUSSION

The Flammulated Owl occurs in two disjunct areas of British Columbia. The major portion of the range is within the dry belt forest of the interior plateau north to 50° 51' latitude. Two records from the Radium Hot Springs area suggest that the Rocky Mountain Trench north to about 50° 40' latitude is the other major area of occurrence in the province. The two areas are about 350 km apart and separated by the Columbia Mountains which reach over 3000 m in elevation and are covered with dense, moist forests at lower elevations. Flammulated Owls have never been recorded from these forest types. Both major areas of the province are northern extensions of dry forest types found in Washington and Montana with no physiographic barriers to the natural expansion of owls from populations in these two states immediately south of B.C.

Table 2.--Survey Route Density Estimates.

Route	Date	Singing Males	Males per 40 ha
Wheeler Mountain	83.06.16	8	.30
Upper Dewdrop	83.06.23	1	.05
Opax Mountain	83.06.29	1	.06
Wheeler Mountain	84.06.25	8	.30
Sabiston Lake	84.06.27	0	.00
Timber Lake	84.06.29	0	.00
Eagle Hill	84.07.09	3	.00
Wheeler Mountain	85.06.20	13	.50
Wheeler Mountain	85.07.05	11	.40
Indian Garden	85.07.09	1	.03

Table 3.--Singing Males Wheeler Mountain Route.

Stop	June 16 1983	June 25 1984	June 20 1985	July 5 1985
1				1
2		1	1	1
3				
4	1			
5			1	
6	2	1	1	
7		1	2	
8	1	1	1	1
9	1	1	2	1
10	1		2	1
11	2	2	2	1
12			1	
13		1	1	
14				
15			1	1
16			2	1
17			1	1
18				1
19				1
20				
Totals	8	8	17 (4 repeats)	11 (2 repeats)

Within the central portion of the range, all records have occurred along the sides of two major intermontane valleys: the Okanagan valley and the South Thompson River valley. Smaller drainages feeding into these larger basins also contain owls. Virtually all of the records have occurred within the distributional limits of the very dry submontane interior Douglas fir forest (IDFa). This open forest occurs as a belt around the sides of major valleys and averages between 850 and 1130 metres in elevation (Mitchell and Green 1981). It lies immediately above the ponderosa pine belt but pine does extend upwards as a seral species after fire or as a codominant with Douglas fir on south-facing slopes. Various authors have recognized the association of Flammulated Owls with ponderosa pine (Winter 1971, Bull and Anderson 1978, Goggans 1986) and a strong preference for foraging in old-growth ponderosa pine - Douglas fir forests (Reynolds and Linkhart 1986). In

Table 4.--Density Estimates Wheeler Mountain Route.

Date	Singing Males	Soundscape	Males Per 40 ha
June 16, 1983	8	450 ha	0.7
June 25, 1984	8	650 ha	0.5
June 20, 1985	13	850 ha	0.6
July 5, 1985	11	1000 ha	0.4

British Columbia, the association with mature-old growth Douglas fir is more clear than the affiliation with ponderosa pine forests. While pine may occur on some sites, it is never a dominant species and usually occurs as isolated veterans well above their normal altitudinal limits. On north-facing slopes, pine is absent but owls are present. Regardless of the presence of pine, the open nature of the fir forests coupled with natural or artificial openings created by logging probably resembles the physical structure of preferred forests in the southern portion of the owl's range. Distribution of the bird in British Columbia is most likely restricted to the IDFa forest belt and equivalent forest types in the Rocky Mountain Trench.

Surveys and random observations near Kamloops confirm a preference for forest in excess of 100 years of age and the highest density of owls occurred in age classes of 140-200+ years with many veteran trees. Selective logging has been a common practice throughout the dry forests of the interior and has resulted in a complex forest structure. The amount of large stems removed varies greatly, depends upon the faller's preference and may reach 80 per cent. The results have been stands with multi-layered canopies and thickets of regenerating firs suffering from crowding and growth restrictions. Owls appear to be restricted to areas with multi-layered canopies and an abundance of large well-spaced trees interspersed with grassy openings up to 2 ha in size. Cavity-bearing snags were moderately common on sites where owls were found. Seven nests were found within the commonly used habitat type. Regenerating thickets were used for roosting but no studies have been done in British Columbia which quantify habitat preference as have been done elsewhere. (Goggans 1986, Reynolds et al. 1987). Random field observations suggest that owls in the fir belt of this province are utilizing the physical characteristics of the forests in similar ways to those noted by Goggans (1986) and Reynolds et al. (1986).

Historical data on Flammulated Owl populations in this province are lacking so it is impossible to say whether the selective cutting practices have resulted in a change in numbers. Several studies have noted a decline in populations following timber harvesting (Marshall, 1957, Phillips et al. 1964, Franzreb and Ohmart 1978). The surveys we conducted were not specifically designed to estimate populations or densities, but some crude estimates were made in order to create a perspective for future studies. On Wheeler Mountain, selectively cut areas appeared to have singing male densities as high as 1.6 males per 40 ha. Transect surveys may have underestimated the real numbers of birds present by as much as 50 per cent, but this may have been due in part to erroneous assumptions made in the surveying procedure. The estimated soundscape surveyed from each stop on the transects was a circle with a radius of 0.5 km. This may be a generous assumption so that density estimates are likely low. Regardless, densities are in the

lower end of the scale reported for this species elsewhere within its range. They compare favorably with estimates of 0.72 singing males per 40 ha in northeastern Oregon (Goggans 1986) and roughly 0.8 per 40 ha in Colorado (Reynolds, Linkhart and Ryder 1986, in press). Densities varied within the total area of Wheeler Mountain. Our transects did not result in a census of the entire mountain, much of which is felt to be suitable habitat. Along transect routes, densities were only 0.4 - 0.7 males per 40 ha. The lowest density was determined from the July 5 survey during which only 1 male was singing voluntarily and was perhaps unmated. The other ten birds were found by playing tape recorded songs. The number of birds responding represents an unknown proportion of the real population but 13 birds were found along the same route two weeks earlier in the same year. The results along other routes should also be considered preliminary. Attempts were made to census only during optimal conditions, but wind noise and light rain were negative factors on some routes. It is felt that the lower densities along routes other than Wheeler Mountain resulted from extensive areas of marginal or unsuitable habitat being surveyed. Once we entered the optimal habitat type, Flammulated Owls were found. The patchy distribution of the habitat is likely responsible for the clumped distribution of owls and may be the reason that birds have been considered loosely colonial (Winters 1974).

Further studies are necessary in order to more clearly delineate the range of this little-known owl in British Columbia. Basic ecological relationships remain poorly understood but it is clear that the bird occupies older forests in areas that are very important to the lumber industry. As currently practised, selective harvesting techniques may enable us to afford this species protection and still manage forests for timber production. The alternative may result in the loss of a unique member of Canada's avifaunal component.

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Censusing Screech Owls in Southern Connecticut¹

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Abstract.--Eastern screech owls (*Otus asio*) were censused in southern Connecticut using playback of tape recorded song. Response frequency and type of response varied seasonally; rates were lowest during the breeding season and highest in fall and winter. Extreme temperatures, certain types and intensity of background noise, and wind decreased response frequency. Tests with radio-marked owls confirmed accommodation of some owls to repeated song playback. Comparison with population estimates obtained using a combination of playback and foot searches suggest that song playback provides estimates within 5-20% of actual screech owl populations.

INTRODUCTION

The eastern screech owl (*Otus asio*) is a small, cryptic owl that ranges from the foothills of the Rocky Mountains to the east coast and northward into adjacent portions of southern Canada. Throughout much of its range it is often the most common bird of prey, occupying a wide variety of habitats in which trees or other structures provide cavities for roosting and nesting. It is also among the most adaptable of raptors to man-modified habitats and may be found in suburban woodlots and the cemeteries, parks and other open spaces of towns and cities.

Despite its relative abundance in suitable habitats this screech owl is rarely noticed because of its nocturnal activity patterns and habit of roosting in concealed locations during daylight hours. Consequently, comparatively little is known of its behavior and population ecology.

Results of a 10 year census of Screech Owls in suburban-rural environments of southern Connecticut using playback of tape recorded song are presented herein. We investigated screech owl response to song playback and census variables such as month,

seasonal activity, moon phase and selected weather conditions. We also noted color phase when possible, and describe perch site selection and behavior of responding owls.

We compared estimates of screech owl abundance determined from playback censuses with estimates based on results of foot searches for roost sites and signs such as pellet deposits, feathers and kill sites.

REVIEW OF LITERATURE

The use of song for acoustic communication in birds has been detailed by Kroodsma et al. (1982) and more specifically for mating and spacing behavior by Catchpole (1982). Eastern screech owls use song for territorial establishment, defense and mating (Bent 1938; and others).

The use of playback of tape recorded song as an avian census technique has been reviewed by Johnson et al. (1981) and Marion et al. (1981) and as a census technique for raptors by Fuller et al. (1981). These authors emphasized the effectiveness of playback in sampling nocturnal or otherwise secretive birds and advocated wider use of this technique to census or locate birds which may respond to vocalizations. Johnson et al. (1981) used song playback to census western screech owls (*Otus kennicotti*) in riparian habitats of southern Arizona; they discovered the highest documented breeding density of screech owls in North America. Other censuses of screech owls using song playback included a fall survey in Michigan (Nowicki 1974), a spring survey in Kansas (Cink 1975) and a 16 week summer survey in Kentucky (Allaire and Landrum 1975).

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Springer (1978) compared response to playback with a visual count of roosts and nests to estimate populations of the great horned owl (Bubo virginianus) in Ohio while McGarigal and Frazer (1984, 1985) evaluated response and habitat use of barred owls (Strix varia) in Virginia. In the last 2 decades playback has also been employed to count owls, mainly screech owls and great horned owls during the annual Christmas bird counts.

STUDY AREAS

Routes for censusing screech owls by song playback were located in the towns of Bethany, Branford, Hamden, Oxford, Orange, East Haven, and Watertown, all in New Haven and Litchfield Counties, Connecticut. Census route details are presented in table 1.

We conducted foot searches for pellets deposited beneath cavities and owls sunning at cavity entrances in Bethany, Oxford and Woodbridge in southern Connecticut and near Elizabethtown, Lancaster County in Pennsylvania. The Pennsylvania study area was described by Smith (1981, 1986). Screech owl accommodation to song playback was tested in New Canaan, Orange and Bethany, Connecticut, during fall and winter months of 1981, 1982 and 1985.

Excepting East Haven, the towns in which the surveys were conducted are suburban-rural habitats with population densities ranging from a low of 173 persons km² in Oxford to a moderate density residential population of 2400 persons km² in Hamden.

The towns lack major industries although a number of small industries are located in several. Habitats of the towns in which the censuses were conducted included wooded areas (38% to 72% of total area of each census route), farmland (0 to 13%), old fields, meadows, pastures (6% to 39.5%), wetland and aquatic habitats (2% to 14%) and residential (6% to 37%).

Historically, most of the study area was farmland and most of the woodlands were clear-cut for farming or for the lumber industry. Although farming is still practiced to some extent in the census areas most of the farmland was abandoned or sold and consequently some of the habitat is in successional stages, principally old field, although much has reverted to woodland. Woodlands in these areas are predominately deciduous and composed of maples (Acer), oaks (Quercus), hickories (Carya), American beech (Fagus grandifolia), white ash (Fraxinus americana) and tuliptree (Liriodendron tulipifera) with understory components of birches (Betula species) and dogwood (Cornus florida). A variety of ornamental trees and shrubs occur in the residential areas.

METHODS

Censusing by Playback of Tape Recorded Song

Census routes in Bethany and Oxford formed a grid pattern with stations located 0.5-1.8 km apart. In other towns, census routes were linear and were selected to ensure adequate coverage of the mix of residential and natural habitats present.

Table 1.--Descriptions of eastern screech owl census routes in southern Connecticut.

Route	Date Started	Date Stopped	Census Interval ¹	Census ² Pattern	Route Length (km)	No. Stations	No. Times Censused	Total Length (km) ³	Total ³ Stations	Observers ⁴
Bethany I	11/11/76	06/23/79	Biweekly	Grid	22.9	24	1	645	645	DGS,DS,MS
Bethany II	12/20/76	05/29/79	Biweekly	Grid	22.4	20	26	472	502	DGS,DS,MS
Bethany III	12/29/79	12/16/81	Biweekly	Grid	20.0	13	34	680	382	DW
Bethany IV	12/27/79	11/07/81	Biweekly	Grid	17.6	13	34	598	442	DW
Bethany V	01/06/82	07/21/85	Monthly	Grid	22.9	24	41	803	850	DGS,MS
Bethany VI	01/12/82	07/06/85	Monthly	Grid	22.4	20	41	781	737	DGS,MS
Branford	10/12/79	09/10/80	Irregular	Linear	11.2	6	16	154	87	DW
Hamden	01/12/80	11/09/81	Irregular	Grid	12.0	9	11	132	98	DW
Orange	02/07/80	02/15/82	Irregular	Linear	8-28.0	9-29	26	493	401	MD,DGS
Oxford I	10/06/76	10/23/78	Biweekly	Grid	28.0	19	43	1202	710	AD,DG
Oxford II	12/28/76	10/05/78	Biweekly	Grid	23.0	15	33	697	456	AD,DG
Watertown	12/27/80	10/02/81	Irregular	Grid	20.3	14	8	156	110	DW
Totals ⁵	--	--	--	--	236.3	188	344	6813	5534	--

¹Census intervals were biweekly, monthly or irregular.

²Census patterns were square grid, circular grid or linear.

³All route census data combined.

⁴Observers: AD, Arnold Devine; MD, Mark Drummond; DG, Debbie Gendron; DGS, Dwight Smith; MS, Maureen Smith; DS, Douglas Spencer; DW, Dan Walsh.

⁵Totals with Orange census route average of 12.8 km and 11 stations.

Stations were spaced approximately 0.7-1.2 km apart, based on a preliminary study conducted by AD in Oxford and Bethany from October through May, 1975-76, and estimates of the size of home ranges of 2 screech owls observed near Elizabethtown, Pennsylvania, by DGS. Results of this study and the sizes of screech owl home ranges determined using radio-telemetry (Smith and Gilbert 1984) in New Canaan, Orange and Bethany, Connecticut, support this spacing.

Exact location of each census station was influenced by its accessibility, proximity to woodlots or ornamentals, houses and parked vehicles and knowledge of previous owl responses.

The pairs of routes in Oxford and Bethany were censused alternately, so that each route was censused biweekly. This time interval was selected on the basis of preliminary studies conducted by DGS and AD in 1975 and 1976 to test accommodation of owls to song playback as a function of time interval between sequential surveys. Censusing of AD and DGS routes was performed in a random starting sequence on alternate weeks to determine if time of night influenced owl response. Censusing of all routes began within 0.5-1.5 hr after sunset.

At each station song playback, included a sequence of whinny and warble songs obtained from the Peterson Field Guide to Bird Songs. Tests conducted along census routes revealed that omnidirectional broadcast of song playback was audible (to us) for a minimum radius of 0.8 km.

Each station was censused for 7-8 min to elicit a vocal or visual response. This consisted of a 1 min listening interval, 5 min song playback interspersed by silent periods of approximately 15 sec and a 2 min listening interval. When an owl responded, the playback was continued for an additional 2 min to elicit response from a second owl. For each response we recorded the number of owls responding, direction of each owl, time interval from first playback to the first visual or audible response and type of response. Owls were illuminated with a flashlight when possible to observe color phase, perch site and behavior.

Variables recorded at the time of censusing at each station were time (EST), sky condition, types and intensities of background noise, moon phase, temperature and wind. Time was recorded as time of first playback. Sky condition was estimated as percent overcast, moon phase was recorded as quarter, half, three-quarter, full and no moon. The sources of background noises were recorded and their intensity estimated on a scale of 1-10 on Bethany census routes conducted by DW and DGS. Temperature was recorded to the nearest 0.5 C. Wind velocity was estimated using the terrestrial application of the Beaufort scale.

Foot and Vehicle Surveys

Foot searches were conducted in 2 isolated woodlots in Pennsylvania, each averaging about 2.59 km² in size and in randomly selected 2.59

km² portions of study areas in Bethany and Oxford. The Pennsylvania surveys were conducted by DGS. Separate surveys in Bethany were conducted by DW, AD and DGS and in Oxford by AD.

In each area we located all tree cavities and other likely roosting and nesting areas such as small, dense conifer stands. These were uniformly searched for signs of screech owls. In Pennsylvania, all cavities were checked by ascents.

Accommodation Tests

To test for accommodation of screech owls to playback of tape recorded song 4 groups, each comprised of 4 screech owls were captured and fitted with radiotransmitters. Owls were captured in roosts, nest boxes and using bal-chatri traps in New Canaan, Bethany and Orange, Connecticut. One owl from each group was censused using song playback at 1 day intervals, 1 at 3 day intervals, 1 at 7 day intervals and 1 at 14 day intervals for 3 months. Censusing of 2 groups was conducted from late September through late December and of 2 groups from November through January. Preliminary studies by DGS and AD had suggested that these were months of uniformly high screech owl response. Prior to each playback, the presence of the screech owl was confirmed by radiotelemetry.

Data Analysis

We used SPSS-X routines (SPSS 1983) for data organization and analysis. Principal components analysis (PCA) was used to search for the variable or combinations of variables which accounted for the highest amount of the total observed variation. Five climate variables (precipitation, cloud cover, wind, sky condition, and temperature), 3 temporal measures (month, time of night and sequence), noise and moon phase were included in the initial correlation matrix. Data entry for the PCA was a subsample obtained by a random sort. The PCA was varimax-rotated to improve interpretation axes.

RESULTS

Playback of Taped Song Surveys

Response Frequency

Screech owl responses were obtained on 37.7% of all calling attempts (2199 responses of 5534 attempts) with all stations on all census routes combined (table 2). At least 1 response was heard at 89.9% of all (169 or 188) calling stations, all routes combined, but the response frequency at each station varied from 3% to 78.8% and averaged 18.2%, suggesting that not all stations were located in screech owl habitat or home range. Thus 11 stations (5.9% of total stations) had a response frequency of less than 5% during the survey while 52 stations (27.7%) had an overall response frequency of over 50%; with the latter station response frequency suggesting the presence of a resident individual or pair.

Table 2.--Summary of eastern screech owl response rates:
by month and census route for southern Connecticut.

Month	Bethany 76-85			Bethany 80-81			Combined ¹			Orange			Oxford			Totals		
	#		Response	#		Response	#		Response	#		Response	#		Response	#		Response
	Sta	#		Sta	#		Sta	#		Sta	#		Sta	#		Sta	#	
Jan	158	84	53.2	102	24	23.5	46	9	19.6	44	16	36.4	46	14	30.6	396	147	37.1
Feb	230	119	51.7	76	19	25.0	49	14	28.5	39	14	35.9	66	26	39.2	460	192	41.7
Mar	404	173	42.8	50	7	14.0	18	6	33.3	61	3	4.9	101	29	28.7	634	218	34.4
Apr	197	51	25.8	46	5	10.8	17	4	23.5	63	6	8.7	93	19	20.2	416	85	20.4
May	168	44	26.1	99	10	10.1	23	2	8.7	40	6	14.8	116	35	30.2	446	97	21.7
Jun	95	50	50.5	118	32	27.1	26	1	3.8	8	3	37.5	98	59	40.2	349	145	41.5
Jul	43	18	42.0	69	8	20.5	26	7	26.9	12	1	8.3	86	36	41.2	236	70	29.7
Aug	132	61	46.2	82	21	25.6	11	7	63.6	---	---	---	100	52	52.0	325	141	43.4
Sep	309	138	44.7	90	26	28.9	14	3	21.4	22	8	36.4	59	27	46.0	494	200	40.5
Oct	228	92	40.4	96	24	25.0	23	13	56.5	46	18	39.1	183	98	53.4	576	245	42.5
Nov	400	253	63.2	55	8	14.5	37	12	32.4	40	21	52.5	136	86	63.4	668	380	56.9
Dec	366	196	53.6	36	18	50.0	5	0	0.0	26	18	69.2	101	47	46.5	534	279	52.2
Totals or Average	2734	1279	46.8	919	202	22.0	295	78	26.4	401	114	28.4	1185	528	44.6	5534	2199	39.7

¹Branford, Hamden, Watertown.

Monthly response frequency followed a seasonal cycle, varying from a low of 20.4% in April (results of all surveys combined) to a high of 56.9% in November. On all census routes the lowest response rates were in April and May while the highest response rates were during the winter months, especially November and December. The period of decreased response frequency occurred during the spring months from late February through May, and to a lesser extent during early summer. This period corresponds with screech owl breeding activities, including egg deposition and incubation, and raising of young in this region, suggesting that screech owls may be secretive during at least part of the nesting season. Allaire and Landrum (1975) also noted a decreased response frequency of nesting screech owls in Kentucky. The increase in response frequency noted during July and August is undoubtedly due to the activities of juvenile screech owls, which have augmented the local populations and are behaviorally often quite responsive during the post-fledging dependency period.

Approximately 14% of the responses were by screech owl pairs. Responses by pairs were recorded from October through June, most frequently in December and March, and were usually more intense and of longer duration than responses by individuals. Slightly less than 4% of responses were by 3 or 4 screech owls. Movements and perches selected by these owls suggested territorial limits, especially when several responses were obtained over a period of 1 or 2 months.

The time interval between the first playback of song and the first screech owl response also varied seasonally. Shortest response times occurred during fall and winter, with monthly averages ranging from 2.34 min in February to 3.05 min in December (table 3). Average response time increased during the spring and summer, with the longest recorded in April, May and June. This seasonal variation occurs synchronously with the

observed variation in overall response frequency and again suggests that screech owls are comparatively reluctant to answer playback of tape recorded song during the nesting season.

Screech Owl Response Forms

Screech owls responded to playback of tape recorded song with a variety of songs and other vocalizations. A few individuals also responded non-vocally; they were observed flying into the immediate area near the broadcasting tape recorder but did not sing or otherwise vocalize.

The most common screech owl response songs were the whinny and warble described by Bent (1938). Individuals in this area showed the greatest variation in the whinny song, which ranged from high to low in pitch and volume and to a much lesser extent varied in duration and number of times repeated. The warble was comparatively uniform in delivery by individuals and consisted of a series of hollow whistles of 1 pitch, separated initially, but merging in a tremolo. Frequently, screech owls responded with a whinny and subsequently switched to the warble song but the reverse also was occasionally noted. Other vocalizations consisted of "screams," "screeches" and bill clacking. The "scream" was occasionally given by juvenile owls and was a shrieking series of mouse-like squeaks, often given during flight. It was typically, but not always, followed by a series of soft whinnies, also given during flight.

Both whinny and warble songs were heard throughout the year, although a seasonal variation in frequency of each was evident (figure 1). During the period after the young had fledged, from June to August, both songs were heard with approximately equal frequency along with a variety of screams, screeches and other vocalizations made by fledged juveniles. Frequency of whinny song increased in August and essentially replaced the warble song throughout the fall and winter months,

Table 3.--Monthly summary of eastern screech owl response time and type, data from all census routes combined.

Month	Response Time (min)			Response Type										N Responses
	\bar{X}	SD	Range	Whinny		Warble		Both		Other		Visual ¹		
				N	%	N	%	N	%	N	%	N	%	
Jan	2.80	1.16	0.1-8.0	74	60.7	11	9.0	35	28.7	0	---	2	1.6	122
Feb	2.34	1.13	0.4-7.1	48	43.6	38	34.4	24	21.8	0	---	0	---	110
Mar	2.84	1.39	0.1-7.5	36	37.9	42	44.2	16	16.8	0	---	1	1.1	95
Apr	3.69	1.56	1.2-8.0	34	24.3	79	56.4	27	19.3	0	---	0	---	140
May	3.65	1.73	0.5-7.4	26	26.0	41	41.0	33	33.0	0	---	0	---	100
Jun	3.17	1.66	0.5-8.0	71	39.7	60	33.5	36	20.1	12	6.7	0	---	179
Jul	3.03	1.33	0.3-7.0	61	40.7	49	32.7	34	22.7	5	3.3	1	0.7	150
Aug	3.09	1.37	0.5-7.0	82	58.6	16	11.4	40	28.6	1	0.7	1	0.7	140
Sep	2.91	1.63	0.5-8.0	109	67.7	18	11.2	33	20.5	1	0.6	0	---	161
Oct	2.67	1.15	0.1-6.0	127	68.3	9	4.8	46	24.7	1	0.5	3	0.6	186
Nov	2.92	1.43	0.3-7.0	70	70.0	4	4.0	24	24.4	0	---	2	2.0	100
Dec	3.05	1.90	0.3-7.0	78	86.7	0	---	8	8.9	0	---	4	4.4	90
Totals	3.01	0.38	0.1-8.0	816	51.9	367	23.3	356	22.6	20	1.3	14	0.9	1573

¹Owls observed that flew into area but did not vocally respond to playback.

suggesting that the whinny song is used extensively for territorial establishment and defense. In late January, frequency of warble song increased and for a brief 2-6 week period both songs were heard with equal frequency on most census routes. From late February through May the warble song displaced the whinny as the most common response

song. The initial vocal responses by a screech owl pair usually consisted of the same song (whinny or warble) although occasionally either the male or female, or both, switched to the other song.

The observed seasonal difference in use of whinny and warble songs is significant when subjected to a chi-square test of a 2 x 12 contingency table (chi-square = 292.37, df = 11, $P < 0.01$). We further tested seasonality of response song by subdividing the contingency table by grouping warble song during the nesting season months (March through May) compared to its frequency during the remainder of the year. The resulting 2 x 2 contingency table chi-square was again significant (chi-square = 121.96, df = 1, $P < 0.01$).

These results agree with earlier comments by Bent (1938) and Hough (1960) regarding the function of the 2 basic screech owl songs. These and other authors and naturalists have noted that the "mating" song (warble) begins in February and is used throughout the spring months, to be replaced by a "territorial" song (whinny) in late summer, fall and winter. Hough (1960) also noted that screech owls near Kripplebush, New York, had a brief silent period in January, but we did not observe this on any of our census routes.

About 0.9% (14 of a sample of 1573 records of response behavior) of the responding screech owls flew directly into the area near to where the tape recorder was broadcasting screech owl songs, but did not respond vocally. These non-vocal individuals were most frequently observed during fall and winter months, suggesting that they may have been young of the year owls without an established territory. However, the lack of a similar frequency of non-vocal individuals during the rest of the year may have been a function of the lack of foliage in fall and winter, which made them more easily observable.

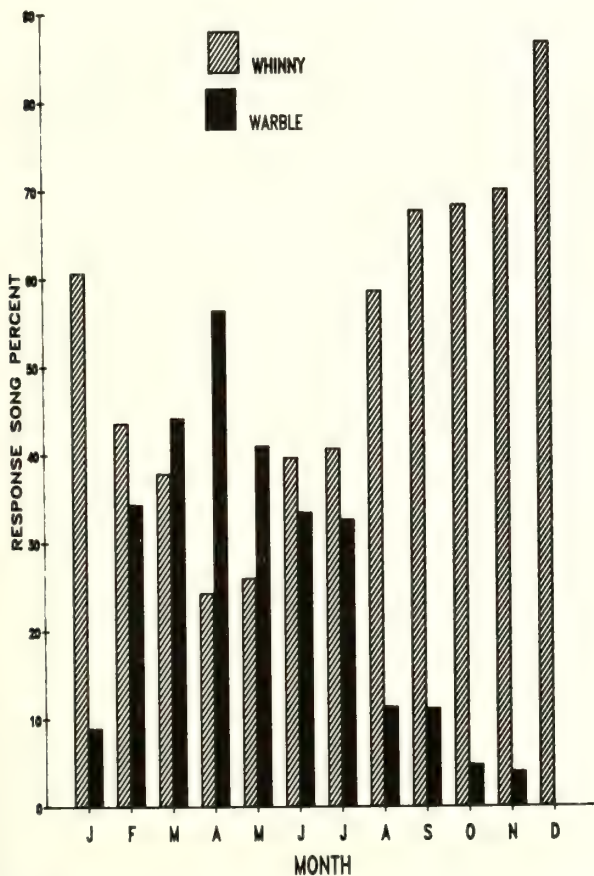


Figure 1.--Monthly frequency of whinny and warble song. Data from all census routes.

Color Phase

Color phase of a responding screech owl was determined when conditions permitted identification. Of 214 owls observed, 150 (70.1%) were gray-phased, 47 (21.9%) red-phased and 17 (7.9%) intermediate. The comparatively low number of intermediate owls actually observed may underestimate the frequency of this color phase in southern Connecticut because several variations of the intermediate color are difficult to differentiate from the gray-phase at night by a flashlight beam. Collectively, the intermediate owls showed a wide variation in color gradation from gray to red, although 3 were the rich "chocolate" or dark brown color.

These figures are approximately consistent with data reported by Owen (1963a, 1963b) who observed a declining frequency of red-phased screech owls northward in eastern North America. The reduced frequency of red-phased owls also agrees with research by Mosher and Henny (1976) who suggested that red-phased screech owls may suffer a higher winter mortality in northern locations due to their significantly higher metabolic requirements at low temperatures compared to gray-phased owls. Van Camp and Henny (1975) observed a higher mortality rate of red-phased screech owls during an especially harsh winter in northern Ohio.

Environmental Factors and Response Frequency

PCA of variables associated with screech owl response frequency results produced 4 factors with eigenvalues greater than 1.0 and collectively accounting for 63.5% of the total variation (table 4). The first factor had high positive loadings for month and sequence; and may be interpreted as an indication of the importance of temporal factors, especially the time of year. A high positive loading for temperature for this factor also would be anticipated, since temperature varies directly with season. The second factor had high positive loadings for precipitation and cloud cover and a high negative loading for wind. These 3 variables are interrelated since cloud cover is, of course, involved in precipitation and both may be accompanied by wind. Therefore we suggest that

this factor represented a climate component. The third factor had high loadings for noise, temperature and time. Noise levels caused by cars and other human activity, wind and insects often decreased during the later evening hours and this factor may, in fact, demonstrate that relationship. The fourth factor is not readily interpretable.

Partial correlations of census variables with screech owl response are presented in table 5. Significant correlations associated with screech owl response include month, sequence and wind. The correlation of response frequency with month reiterates the seasonal change in screech owl response frequency described previously. The relationship with sequence is especially important because it indicates some degree of accommodation by screech owls to playback of tape recorded song which must be considered when censusing of this owl will be conducted for an extended period of time. Wind negatively influenced screech owl response. Although our radiotelemetry studies indicated that screech owls did leave their roost sites regardless of wind conditions they may have decreased their foraging activity as wind velocity increased, perhaps because of inherent foraging difficulties. As a negative factor, wind is probably even more important than indicated by this

Table 4.--Factor matrix of variables associated with number of screech owl responses obtained during censusing.

	Factor 1	Factor 2	Factor 3	Factor 4
Month	.769	.005	-.107	.147
Temperature	.583	.276	.555	-.157
Precipitation	.059	.723	-.443	.064
Cloud Cover	.312	.711	-.110	-.023
Noise	.283	.284	.596	.197
Sequence	.788	-.118	.522	.397
Time	-.206	.309	.427	-.674
Wind	-.129	-.676	-.005	.530
Moon	.274	-.035	-.244	-.386
Variance %	19.4	16.0	15.5	12.6
Cum. Variance	19.4	35.4	50.9	63.5

Table 5.--Linear Correlation Coefficients (Lower Left) and Partial Correlation Coefficients (Upper Right) of Census Variables¹

	Response %	Month	Time	Sequence	Temp	Moon	Wind	Cloud	Noise	Precip
Response %	--	-.1601*	-.0567	.1183	.0650	-.1013	-.5518**	.0153	-.0843*	.0747
Month	.3159**	--								
Time	-.0104	-.2531	--							
Sequence	-.2150**	.0689	-.0221	--						
Temp	.2114**	.0798	-.0719	-.0992	--					
Moon	.1137	.1135*	-.1426*	-.0233	.1557*	--				
Wind	-.3420**	-.1020	-.0065	-.0064	-.0288	-.0059	--			
Cloud	.0952	.1628**	.0049	.0132	.0703	-.0570	-.0077	--		
Noise	-.3117**	.0156	.1184	.1015	.2140*	-.1586	.3255**	-.0511	--	
Precip	.0174	.1990**	-.0039	-.0516	.0253	-.0594	-.1200*	.0780*	.3024*	--

¹Probability Levels: * P < 0.05; ** P < 0.01.

partial correlation; we occasionally terminated our surveys early on windy nights because of exceptionally poor response frequency. The lack of a significant correlation with moon phase is interesting; anecdotal accounts by Leon Kelso (pers. commun.) and others suggest that screech owls are especially active and responsive on full moon nights, but we have been unable to confirm this. Results of a separate study conducted by Pat Lynch (1982) with DGS concerning response of urban open space screech owls in southern Connecticut also failed to indicate a correlation between screech owl response frequency and moon phase.

The behavior of responding owls varied to some extent with weather conditions. On bright, clear nights with a three-quarter or full moon responding owls were generally reluctant to approach the speaker and their response duration was usually brief. In contrast, on dark, cloudy or foggy nights responding owls were more aggressive, approached the speaker and remained in the vicinity longer, frequently singing.

A semiquantitative treatment of the relationship between 9 sources of noise and response frequency is illustrated in figure 2. Several of the background noises most frequently recorded at census stations were seasonal; insect noise was recorded at almost every station during late spring, summer and early fall; while amphibian noise was usually recorded in spring. Aircraft and car noise was recorded at almost every station throughout the year: the study areas were bisected by several roads and located near several private and commercial airports.

Comparison of response frequency at "quiet" stations with "noisy" stations confirms that noise negatively affects response frequency and suggests that a variety of noises might act individually or in combination. There is no obvious difference in affect of man-caused noise such as voices, cars or airplanes and natural noise; this, however, is not unexpected since the census areas are located in suburban rural habitats and we may presume that resident screech owls are accustomed to such noises. Therefore, we are unable to determine noise related decrease in response frequency is due to disturbance factors, inability of the screech owl to hear the song playback, or our inability to hear the screech owl response.

Accommodation

The responsiveness of radiomarked owls to test accommodation varied directly as a function of the frequency of song playback surveys. Screech owls censused on 1 and 3 day intervals showed less than 15% overall response rate during the 3 month testing period with only 2 exceptions while owls censused at 14 day intervals showed the highest overall response rate throughout the censusing period (figure 3). In addition, we noted that most of the responses by screech owls censused at 1 and 3 day intervals occurred during the first 2 or 3 weeks of censusing, thereafter they seldom responded although radiotelemetry confirmed their presence

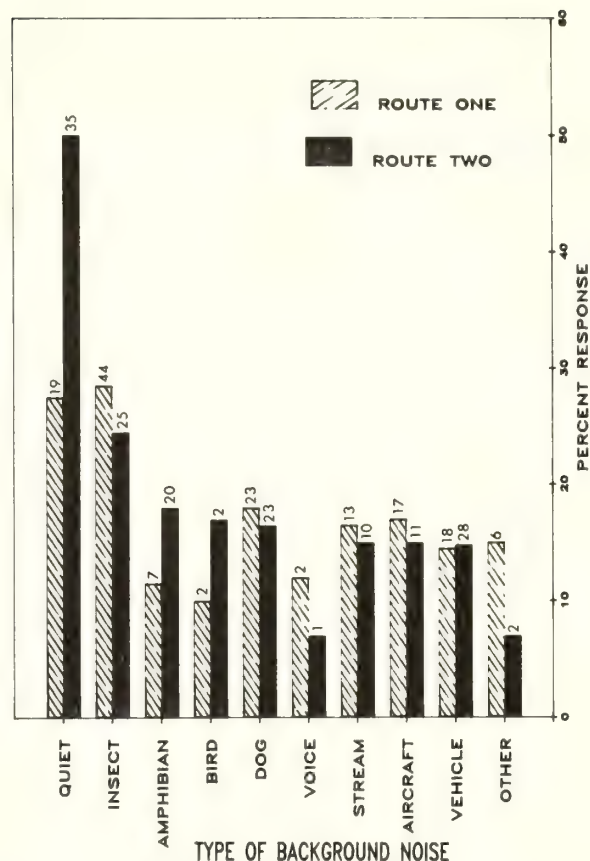


Figure 2.--Relationship between observed response frequency and types of background noise. Data from census conducted by DW. Numbers represent observed incidence of background noise.

within their home range. Conversely, owls censused at 7 and 14 day intervals showed a much greater uniformity of response during the test period. Smith (1979) found a similar decrease in barred owl response frequency when censused at daily intervals in late summer in northeastern Pennsylvania.

Perch Site Selection

Perch site selection by eastern screech owls responding to playback of tape recorded song was determined, when possible, on surveys conducted by DW and DGS (table 6). Totals for each category of information represent observations for that category and overall totals may therefore differ among categories.

No significant differences were detected in perch sites selected by red and gray-phased owls, when values are weighted for the differences in color phase sample sizes. Preston (1980) described differential perch site selection by color morphs of the red-tailed hawk (*Buteo jamaicensis*) and proposed that perch sites were selected to maximize concealment from potential prey. Color morphs of screech owls, however, lack distinct light and dark phases and this, plus their nocturnal activity patterns may negate the need for

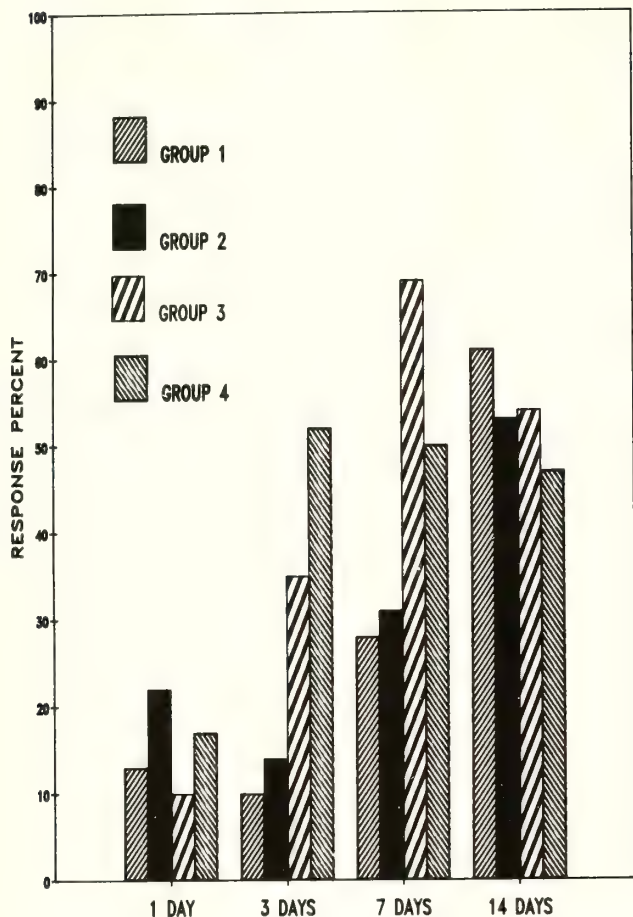


Figure 3.--Relationship between response frequency and censusing interval to test accommodation of eastern screech owls to playback of tape recorded song.

differential perch site selection by the red and gray-phased individuals. It should be noted however, that this applies only to screech owls responding to playback of tape recorded song and not owls actively foraging or roosting.

Perch heights of responding owls averaged 4.65 m and ranged from 1.5 to 11.0 m, although considerable variation was observed. Perch sites were mainly trees (92.1%) although telephone lines, poles, fence posts, concrete abutments and buildings were infrequently used. Almost 75.1% of trees in which screech owls perched had a dbh of 22.9 cm or smaller, reflecting a selection of saplings and relatively young trees. However, trees of this size commonly represented the most abundant component of woodland understory and ornamentals planted in yards.

Basically, responding owls chose perch sites which afforded both protection and concealment; they tended to avoid selection of isolated trees, high perches in mature trees with a relatively open canopy and very low perch sites. Thus the perch sites chosen provided good platforms for broadcast of response song while simultaneously offering maximum concealment from potential predators.

Other Responding Species

At least 13 other species responded to playback of eastern screech owl song, including 3 species of owls (table 7). Responses by other owls were heard mostly during winter and early spring months from October through March while responses by avian species other than owls were heard during spring and summer months. Great horned owls responded most frequently (14 of 62 recorded responses by species other than screech owls), especially during their period of territorial establishment and defense which occurs in this area from December through March. At least 1 great horned owl responded by flying to an overhead tree limb which had previously been the favorite response perch of a screech owl responding to DGS broadcast. The great horned owl sat quietly on the limb for several min during and after playback, then flew away. Subsequently, DGS did not obtain a screech owl response in this territory again for over a year, suggesting the possibility that at least some great horned owls will attempt to prey on singing screech owls.

American woodcocks were heard on censuses conducted separately by DGS, DW and AD during May and whip-poor-wills were heard during May and June. Woodcock migrate into southern Connecticut in late March and whip-poor-wills in early May: both species are vocally aggressive during the late spring and early summer months. Screech owl song most commonly elicited responses by a variety of passerines (32 of 62 responses), of which we were able to identify 6 species. Of these, mockingbirds (*Mimus polyglottos*) were the most responsive, especially during May and June. On 22 May 1978 a mockingbird was heard singing on AD arrival at a screech owl survey station prior to the use of playback. After playing the screech owl song the mockingbird subsequently imitated a crow (*Corvus brachyrosus*) call, and continued until he departed (Devine, 1982).

Population Estimates Using Song Playback

Estimates of screech owl population density are difficult to obtain because of inherent variables in response frequency caused by weather, seasonal variation in owl responsiveness and accommodation. We chose to estimate screech owl abundance during fall and early winter months, from October through January. The screech owl population density, augmented by addition of young of year, is highest at this time and both adults and yearlings are behaviorally most responsive to song playback.

We made several assumptions when determining screech owl density in the census areas including (1) census stations were spaced equidistant within the grid system, so that separate areas were censused by each station (2) stations with a total recorded screech owl response frequency of 50% or greater during the fall and winter survey were assumed to have resident owls or (3) stations with a response frequency of 35% or greater during every month were assumed to have resident owls.

Table 6.--Summary of perch sites used by responding eastern screech owls. Data from censuses conducted by DW and DGS. Percentages are in parenthesis.

Color Phase ¹	Height of Perch (m)				Type of Perch							
					Tree		Post		Line		Other ²	
	N	X	SD	Range	N	%	N	%	N	%	N	%
Gray	78	4.79	2.6	1.5-10.6	78	48.3	2	1.3	2	1.3	1	0.5
Red	34	4.12	2.9	1.4- 8.2	33	21.9	0	---	0	---	1	0.5
Unknown	39	5.03	3.1	1.9-11.0	33	21.9	3	2.0	1	0.5	2	1.3
Total	151	4.65			139	92.1	5	4.3	3	1.8	4	2.3

Color Phase ¹	Tree Size Class ³								Type of Limb					
	A		B		C		D		Horiz		Vertical		V-crotch	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Gray	48	40.7	7	6.1	2	1.7	2	1.7	46	38.3	7	5.8	2	1.7
Red	6	5.2	9	7.8	9	7.8	1	0.8	25	20.8	3	2.5	10	8.3
Unknown	16	13.9	12	10.4	3	2.6	0	---	23	19.2	2	1.7	2	1.7
Total	70	60.9	28	24.3	14	12.1	3	2.6	94	78.3	12	10.0	14	11.7

Color Phase ¹	Tree Species														
	Red Maple		Sugar Maple		White Oak		Red Cedar		Birch sp.		Apple		Other ⁴		
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	
Gray	16	15.1	3		2.8	5	4.7	3	2.8	3	2.8	7	6.6	15	14.2
Red	8	7.5	3		2.8	1	0.9	2	1.9	1	0.9	1	0.9	9	8.5
Unknown	3	2.8	3		2.8	3	2.8	1	0.9	5	4.7	1	0.9	14	13.2

¹Intermediates included with red-phased owls.

²Other observed perches included telephone poles (2), top of van (1), car top (1).

³Tree size classes were: A = 3-9 cm; B = 10-20 cm; C = 21-33 cm, D = 33+ cm; diameters.

⁴Other species included Black Locust (1), Black Oak (1), Black Cherry (3), Witch Hazel (1), Red Pine (2), ornamental conifers (3), ornamental hedge (2).

Results of our population estimates for the 3 survey areas are presented in table 8. Density estimates on the study areas ranged from 1.41 owls/km² in Bethany to 0.63 owls/km² in Oxford. These estimates are considerably higher than reported in other studies of eastern screech owls. In Michigan, Nowicki (1974) recorded a screech owl population density of 0.88 owls/km², whereas Craighead and Craighead (1956), using foot searches, reported densities ranging from 0.24 owls/km² in 1941 to 0.38 owls/km² in 1947 and 1948. In northeastern Kansas, Cink (1975) determined a population density of 0.1-0.35 owls/km² by song playback. Nowicki (1974) and Cink (1975) suggested that there is a significant relationship between screech owl abundance and percentage of available habitat as woodland. Correlation of our density estimates with amount of woodland in each of the study areas was significant ($r = 0.788$, $P < 0.05$), thus providing additional evidence for this relationship.

The accuracy of estimates obtained by song playback censuses varied considerably when compared with estimates obtained by a combination of song playback and foot searches and with foot searches alone. Near Elizabethtown, song playback coupled with visual sightings indicated a density of 1.2 owls/km² in the isolated woodlots while census results were 1.09 owls/km², a difference of less than 10%. Foot searches alone revealed a density of 0.5 owls/km², a 59% difference. Comparative results

for Bethany, show similar discrepancies in accuracy of each of the 3 methods. In Oxford, AD determined a screech owl abundance of 1.54 owls/km², which was 58% higher than estimates determined on song playback census routes. Use of foot searches alone provided positive evidence of less than 0.45 owls/km² at Elizabethtown and 0.2 owls/km² in Bethany, both of very questionable percentage.

ABUNDANCE ESTIMATES BY LOCATING SCREECH OWLS AT CAVITY ENTRANCES

Craighead and Craighead (1956) estimated screech owl populations on their Michigan study area by observing individuals "sunning" at cavity entrances. While this method presumably works well in areas where woodlots are small, easily accessible and suitable roosting cavities readily located and monitored, it is very difficult to apply in southern Connecticut and other areas of woodland which offer a larger number of cavities.

We tested use of this method in southern Connecticut and near Elizabethtown, Pennsylvania by (1) observing the frequency of sunning by radio-transmitter equipped screech owls at different roosts and (2) monitoring individuals known to be using specific roost cavities to determine how frequently they were sunning at cavity entrances during daylight hours.

Table 7.--Responses to playback of taped song of eastern screech owls by other species. Data is from Bethany and Oxford census routes.

Species	Month										Total
	Jan	Feb	Mar	Apr	May	Jun	Aug	Oct	Dec		
Great Horned Owl (<u>Bubo virginianus</u>)	5 ¹	3	2				1	1	2	14	
Barred Owl (<u>Strix varia</u>)				1	2			1	1	5	
Saw-Whet Owl (<u>Aegolius acadicus</u>)		1 ²								1	
American Woodcock (<u>Philohela minor</u>)					6					6	
Mourning Dove (<u>Zenaida macroura</u>)						1				1	
Whip-poor-will (<u>Caprimilgus vociferus</u>)					1	2				3	
Mockingbird (<u>Mimis polyglottos</u>)					1 ³	5				6	
Catbird (<u>Dimetella carolinensis</u>)						1				1	
Black-Throated Green Warbler (<u>Dendroica virens</u>)						2				2	
Ovenbird (<u>Seiurus aurocapillus</u>)					1					1	
Cardinal (<u>Cardinalis cardinalis</u>)				1						1	
Field Sparrow (<u>Spizella pusilla</u>)					1					1	
Unidentified Anseriformes			1							1	
Unidentified Passeriformes		1	6	1	1	8	1	1		19	
Totals	5	5	10	2	13	19	2	3	3	62	

¹ Great Horned Owl response was visual.

² Saw-Whet Owl was observed at a census station.

³ Mockingbird imitated crow after playback of tape.

Of 4 radiotransmitter equipped screech owls for which we have 7 or more roost site records, a female monitored for approximately 14 months was observed sunning at 9 of 15 (60.0%) regularly used roost sites. Another, a male monitored for 4 months, was observed sunning at 3 of 7 (42.9%), while 2 monitored during February and March used

2 of 7 (28.6%) cavities for sunning, apparently regardless of weather conditions. Collectively, these records suggest that probably most or all screech owls do exhibit sunning behavior at suitable roost cavity entrances. However, they also suggest that not all roost sites may be used for sunning.

Table 8.--Comparison of screech owl population density estimates obtained by song playback surveys, combination surveys and on-foot surveys. Data from censuses conducted by DGS and AD.

Survey Area	Song Playback Owls/km ²	Combination Owls/km ²	On-Foot Owls/km ²	% Diff. ¹	% Woodland
Bethany	0.92	1.18	0.3	21.9	71.4
Elizabethtown	1.05	1.20	0.5	9.0	89.6
Oxford	0.63	1.54	---	40.9	71.5

¹Percent difference between density estimates obtained by song playback surveys and combination surveys presented.

Daylight sunning of screech owls appears to be a function of several variables, including disturbance levels near the roost site, weather conditions and individual behavior. Generally, screech owls sun or at least appear at roost site entrances more frequently during afternoon and early evening hours compared to morning hours (table 9). Almost all screech owls appeared at cavity entrances for at least a brief period during the evening hours after sunset but before total darkness.

Individuals sunning varied considerably in their tolerance of types and intensities of disturbance. Three were exceptionally tolerant; all had roost sites in large maples adjacent to busy roads and would sun at the cavity entrance even during periods of busy traffic. Of these, 1 was located about 6 m from a multi-family unit house. This individual was accustomed to and tolerant of a variety of activities on the sidewalk directly beneath the roost such as children playing, adults parking cars and walking up to the roost tree and dogs barking nearby. The other 2 owls, however, were tolerant only of moving cars and people jogging by below. If cars slowed or stopped in the immediate vicinity of the roost sites the owls would drop into the cavity. Most of the other individuals observed at roost site entrances were much less tolerant of human activity and would drop into the cavity as soon as we appeared or were heard. Again, tolerance appeared to be a function of the particular roost site selected to at least some extent. The previously noted transmitter-equipped female which was exceptionally tolerant while in the high roost cavity adjacent to the roadway was easily disturbed when occupying some other roost sites such as nest boxes and low snags and was never observed at a few sites.

We were unable to obtain reliable density estimates of screech owls using this technique, even in the relatively small study areas in which it was applied. In Elizabethtown, only 1 roost was discovered although the singing incidence of owls suggested a much higher local abundance. In southern Connecticut we located 15 of 250 (6%) of screech owl roost sites by observation of sunning owls. We were unable however, to locate roost sites of

owls which, on the basis of repeated playback surveys, were known to be within a specific area, quite possibly because of the need to check most cavities by foot searches, which results in unavoidable noise which in turn might disturb the owls. In summary, we are unable to recommend this method for estimating screech owl abundance.

MANAGEMENT IMPLICATIONS

Censusing eastern screech owls using playback of tape recorded song provides a quick, relatively easy method for obtaining indices of population abundance, even by relatively untrained personnel. Censuses repeated at time intervals sufficient to decrease accommodation to song playback provide consistent results which can be used to determine trends in seasonal and annual abundance, when weather and behavioral variations are considered. The only alternative methods that can provide similar information are extremely time consuming, require individuals with a considerable degree of expertise, and should be repeated at reasonable intervals to obtain accurate abundance estimates. Information provided by song playback can also be used to evaluate correlations between screech owl abundance and habitat variables.

To some extent certain aspects of the screech owl population may be ascertained using song playback including (1) time of pairing or intensity of the pair bond as determined by weeks in which pairs respond at particular stations (2) approximate home range estimates where individuals visually observed have distinctive plumage patterns or distinctively pitched song and (3) information on boundaries of home ranges, where adjacent pairs respond simultaneously to the song playback.

The feasibility of song playback censuses to estimate owl abundance may best be illustrated using examples from our studies. Song playback revealed the presence of a minimum of 2 individuals each on 2 woodlots near Elizabethtown, Pennsylvania. All 4 owls were visually observed in early evening hours several times over a 3 month period, confirming their use of the isolated woodlots.

Table 9.--Observed frequency of eastern screech owls "sunning" at cavity entrances.¹

Time ²	January	February	March	April ³	November	December
0530-0729	2/18 (11.1)	1/ 7 (14.3)	--	0/3 (0.0)	--	0/ 8 (0.0)
0730-0959	4/27 (23.5)	3/16 (18.8)	--	--	--	0/ 4 (0.0)
1000-1259	15/27 (55.6)	7/12 (58.3)	3/ 7 (42.9)	--	--	2/11 (18.2)
1230-1359	20/42 (47.6)	7/12 (58.3)	--	2/5 (20.0)	--	4/ 7 (57.1)
1400-1629	18/27 (66.7)	10/13 (76.9)	10/17 (58.8)	2/3 (66.7)	6/12 (50.0)	13/17 (76.5)
1630-Dark	21/30 (70.0)	11/12 (91.2)	12/14 (85.7)	3/3 (100.0)	9/ 9 (100.0)	10/16 (62.5)

¹Numbers represent owls observed at entrance per known owl roostings, percent in parenthesis. Totals vary as a function of the number of times we were able to check a known owl roost each day.

²Includes observations recorded only on uniformly sunny days.

³All observations for this month were of a male.

DGS attempted to locate the roost sites of these owls during daylight hours by searching for pellet depositions, owl feathers and owl kills. Only 1 of the 4 was located in approximately 250 man hours, although all observed cavities were checked by ascents from 3 to 8 times during the 3 month period. In Oxford, AD found a pair that consistently responded within 10-50 sec to playback over a 12 day period. AD unsuccessfully spent approximately 30 hrs over a 3 week period attempting to locate a roost, by screech owl pellet deposition, signs of whitewash, screech owl feathers or kills.

The results of our studies lead us to suggest that playback provides the only effective method for estimating screech owl populations in our study areas in Pennsylvania and southern Connecticut. Furthermore, our synchronous attempts at obtaining population indices with a combination of alternative methods lead us to suggest that it is virtually impossible to obtain accurate indices of screech owl abundance by using any other method or combination of methods in extensively wooded areas.

SUMMARY

We surveyed eastern screech owl populations in southern Connecticut using song playback. Song playback provided consistent information on presence and abundance of screech owls throughout the year. Screech owls exhibited a seasonal frequency of response to playback, being most responsive during fall and winter months and less so during spring and summer. Response to song playback varied significantly with time of year, sequence and noise levels but not with weather conditions or moon phase.

The variation in screech owl response frequency with survey sequence suggests that at least some individuals may accommodate to song playback. Accommodation tests using radiomarked screech owls confirmed that some individuals accommodate to playback as a function of censusing frequency; owls censused at 7 and 14 day intervals showed much greater overall response rates compared to owls censused at 1 and 3 day intervals.

Population estimates obtained during fall and winter indicate sizeable screech owl populations that vary in density as a function of percent woodland. Comparison with population estimates obtained by a combination of playback, foot searches and visual confirmation suggests that song playback provided estimates within 15-30% of actual screech owl populations during months of maximum screech owl response.

We were unable to confirm reliability of counts of owls sunning at cavities during daylight hours as a method for locating and estimating screech owl populations.

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Status of the Eastern Screech Owl in Saskatchewan with Reference to Adjacent Areas¹

Christopher I. G. Adam²

Abstract.--In 1985 and 1986, the author conducted censuses of Eastern Screech-Owls in southeastern Saskatchewan using tape playbacks. The survey, along with other recent and historical records, contributes to the first delineation of the species' range in Saskatchewan. The Saskatchewan population lies at the northwestern extent of the species' range in North America, and is placed in a regional context by examining the occurrences of the screech-owl in Manitoba, Montana, North and South Dakota and Alberta.

INTRODUCTION

In Saskatchewan, the Eastern Screech-Owl (*Otus asio maxwelliae*) is a rare resident of riparian habitat in the southeastern portion of the province, chiefly along the Souris River, Wascana Creek near Regina, and north to Yorkton and Duck Mountain Provincial Park. To date, very little has been published concerning the status of screech-owls in western Canada. Penak (1985)³ summarised the knowledge of the Canadian range of the species.

The Eastern Screech-Owl is common throughout most of eastern North America from southern Manitoba south to Texas. It reaches the northern extent of its range in southern Ontario and Manitoba. The range of the Western Screech-Owl (*O.a. kennicottii*), which was recently split from *asio* (American Ornithologists' Union 1983), extends into western Montana and the western and southern interior of British Columbia (Godfrey 1986) south to Mexico.

Otus asio is a small arboreal horned owl which stands about 22 cm tall. In Saskatchewan, the *maxwelliae* subspecies exists in two colour phases, pale gray and the rarer pale red. In the

prairies, the screech-owl is restricted to tree cavities in riparian Manitoba maple (*Acer negundo*) habitat.

Censusing screech-owls by playing tape recorded calls has been used by Carpenter (these proceedings) in Michigan; Cink (1975) in riparian woodland in Kansas; Johnson et al. (1981) in riparian woodland in Arizona; Lynch and Smith (1984) and Smith et al. (these proceedings) in urban open-space areas Connecticut; Nowicki (1974) in Michigan; and Youmans along the Yellowstone River in Montana⁴.

Eastern Screech-Owls are one of three owl species which respond well to tape playbacks (Smith and McKay 1984). Although both sexes sing, it is by no means certain that only males respond. However, when a single owl responds to the taped call, it is likely the male of a presumed pair rather than an unmated bird. Caution must be exercised in the interpretation of results as it cannot be assumed that each owl responding is paired, or that there are no owls present if there is no response. McNicholl (1981) cautioned researchers using tape censusing techniques that there may be a seasonal variation in response to taped calls resulting in distortion of results.

This paper summarises the status of the Eastern Screech-Owl in Saskatchewan, reports on surveys conducted by the author along the Souris River in 1985 and 1986, and compares the Saskatchewan range with that in the neighbouring states and provinces of Manitoba, Montana, North and South Dakota and Alberta.

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METHODS

The 1985 and 1986 Censuses

In 1985, the author co-ordinated a census of Eastern Screech-Owls in southern Saskatchewan for the Saskatchewan Natural History Society (SNHS). This census took place in March and April of 1985 and used volunteers gathered mostly from the SNHS membership. A second census took place in March and April of 1986 with some of the same volunteers participating. Volunteers were assigned different areas of the province, and were supplied with topographic maps for each area, a set of instructions, and a tape of owl calls.

The Souris River Valley between Estevan and the U.S. border (figs. 1 and 2) was censused by the author between April 9-12, 1985 and April 21-24, 1986, from dusk until about midnight. Although most suitable habitat was surveyed, some was inaccessible due to the absence of roads or trails. The ideal survey situation, a stop every 0.5 kilometres, was impossible due to the sometimes limited access to the best river valley habitat.

At each stop, the owl tape was played and responses, if any, were noted and mapped. The owl call sequence used consisted of three "whinny" calls (descending trills), a "bounce" call and a "trill" (monotone trill) (Cornell Laboratory of Ornithology 1983). At each stop, complete sequences were played until a response was elicited or until a total of five sequences failed to elicit a response. Usually five to ten minutes was spent at each stop.

The same methods were used in 1986, except that the number of stops was reduced by eliminating areas of unproductive habitat. Calling owls were tracked down and observed by flashlight in the last two nights. This method

required that the forested habitat be approached or entered rather than being censused from a road.

Although attempts were made to resurvey the areas in 1986 using the same volunteers, response to the survey was much lower. A media campaign conducted by the author produced some interesting records from members of the public. Letters were sent to various weekly and daily newspapers in the southeastern portion of the province, and a radio interview was conducted.

The Study Area

The Souris River, from its source near Weyburn in Saskatchewan, flows southeastwards through some excellent but discontinuous screech-owl habitat east of Estevan to the U.S. border where it continues into North Dakota. Southeast of Minot (and the junction of the Des Lacs River), it swings east then north and skirts the west side of the Turtle Mountains before entering Manitoba where it joins the Assiniboine River near Brandon.

The Souris River study area (fig. 2) consisted of about 95 kilometres of meandering river within a broad valley in the Mixedgrass Prairie Ecodistrict (Harris et al. 1983) of southern Saskatchewan, between Estevan and the Saskatchewan - North Dakota border. The typical habitat along the Souris River, and in all other areas where the author has heard screech-owls, is a continuous or discontinuous Manitoba maple river bottom woodland (fig. 1) within a meander or curve, and situated so that the meander creates a discrete patch of woods. The maples are mature and large, with twisted branches and numerous natural cavities.

SURVEY RESULTS

The Souris River Study Area

Between April 21 and 24, 1986, a total of 17 singles or pairs were heard and/or seen by the author and S. Fitzgerald in 53 stops between Estevan and the US border, compared with 8 in 1985 in 85 stops (table 1). All owls appeared to be the pale *maxwelliae* subspecies.

Owls responding to the taped calls approached to within 7 or 8 metres and usually sat on an exposed branch within 3 or 4 metres of the ground. A second team member was easily able to zero in on the call and locate the owl by flashlight. This proved to be an excellent way to determine the colour phase of the owl. The calls were not loud, and gave the impression that the owl was calling from several hundred metres away. Out of 8 owls censused in this way, 7 were actually observed. Approximately 90% of tape-attracted screech-owls can be seen this way but care must be taken not to alarm the owl or this method will be unsuccessful. In neither year were the owls calling on their own volition since April is a relatively late date to be censusing owls in Saskatchewan.



Figure 1.--Riparian Manitoba maple habitat along the Souris River east of Pinto, Saskatchewan.

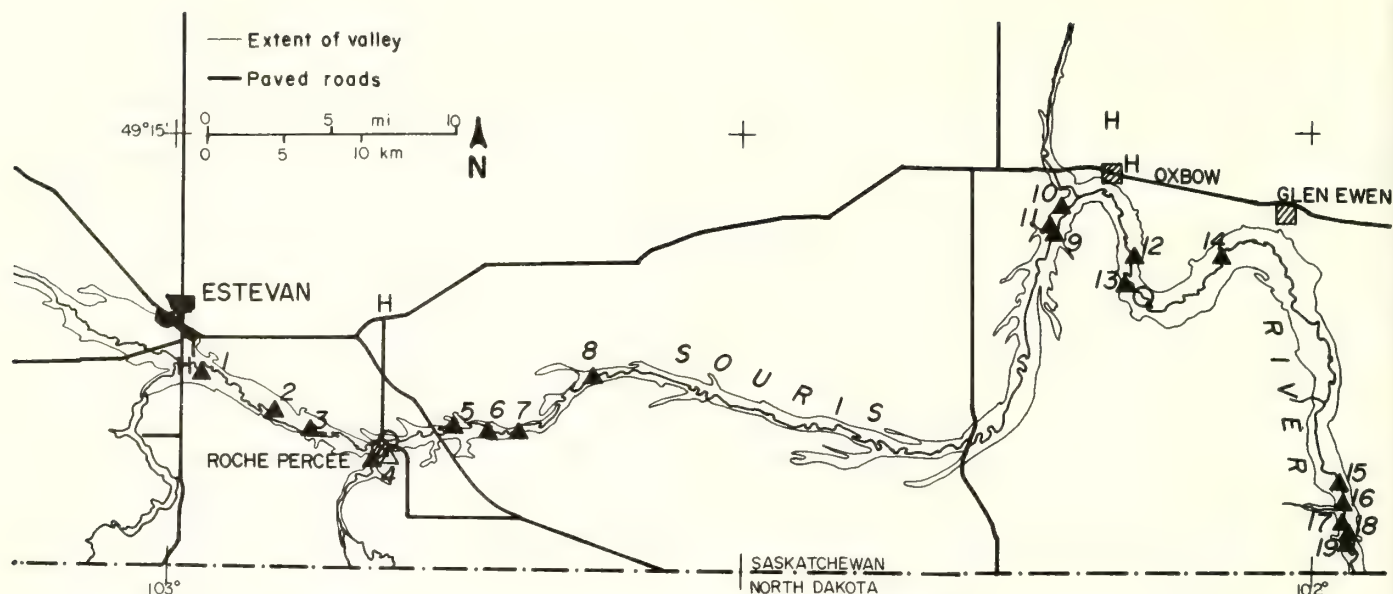


Figure 2.--The Souris River Study Area, Saskatchewan. ▲ = territorial records corresponding to the text and table 1. Additional records not mentioned in the text: H = hypothetical, O = pre-1979 non-territorial, and △ = pre-1979 territorial records.

There seem to be a number of "hotspots" in the Souris River for screech-owls, interspersed with areas of poor or no habitat (fig. 2). These are: (1) the Estevan to Pinto area, including Roche Perceé; (2) the Oxbow area; and (3) the area south of Glen Ewen at the US border. Of the 8 owls seen, 1 was a probable gray-phase, 5 were definite gray-phase and 2 were red-phase. Both red-phase owls were at the Glen Ewen location.

The best responses to taped calls came early in the evening, until about two hours after sunset. It is, however, dangerous to draw any conclusions from this observation for three reasons: (1) the census was usually concluded around midnight, thus no responses were obtained for the remainder of the night; (2) since this is a dispersed population, the observers may have hit portions of the study area with no owls at about the time the responses seemed to taper off; and (3) the sample size was very low on any given night.

The majority of owls were associated with farms with haystacks and/or feedlots, or were near villages or houses. It may be significant that a long, mostly uninhabited stretch of the Souris River between Oxbow to about 16 kilometres south of Glen Ewen produced only one response. However, the stretch of the river immediately north of the U.S. border, south of Glen Ewen, had the densest population of screech-owls in the entire study area, about one territorial owl per 1 kilometre (compared to one owl per 3 or 4 kilometres in the rest of the study area).

The population in Saskatchewan appears to be low and scattered, as would be expected at the northwestern extent of the species' range. The total Saskatchewan population is "guesstimated" at 30 to 35 pairs, and is certainly no more than 50 pairs. Although the Souris River population seems to have increased, the increase is no doubt due to more efficient census techniques rather than an actual increase in birds.

DISCUSSION

The Range of the Eastern Screech-Owl in Western Canada and the U.S

The American Ornithologists' Union (1983) lists the range of both species of screech-owl in the relevant western states and provinces as follows: Eastern Screech-Owl - "Resident from southern Saskatchewan (probably), southern Manitoba, ... west to eastern Montana, the Dakotas ... Recorded in summer (and probably breeding) in central Alberta"; and Western Screech-Owl - "Resident from ... western Montana" south to southern Baja California.

The ranges of both species will be briefly examined for Saskatchewan, Manitoba, North Dakota, South Dakota, Montana and Alberta. The range in Saskatchewan is based upon a complete analysis of all records. The ranges in the remaining areas utilize personal communications, the relevant literature, and seasonal reports and Christmas Bird Count (CBC) summaries in American Birds (AB) and Audubon Field Notes (AFN). Some early

Table 1. Summary of 1985 and 1986 Souris River Screech-Owl censuses between Estevan - Roche Percee (ERP) and Oxbow - Glen Ewen (OGE). w = "whinny" (descending trill), and t = "trill" (monotone trill). A number of entries separated by commas indicates the number of different owls calling. Observers: C. Adam, S. Fitzgerald, except ERP 11 and ERP 15. Under Location, e refers to east of a given location, w to west of, etc. Numbers in brackets refer to mapped locations in fig. 2.

Date	Year	Stop#	Ref.No.	Location (1-19)	Calls	Phase
Apr 21	86	86-3	ERP 03	Estevan (1)	lw,lt	
Apr 09	85	85-13	ERP 04	se of Estevan (2)	3w	
Apr 21	86	86-5	ERP 05	se of Estevan (2)	t	
Apr 21	86	86-7	ERP 06	se of Estevan (3)	t	
Apr 09	85	85-22	ERP 10	Roche Percee (4)	w,t (pair)	
May 25	85	---	ERP 11	e of Roche Percee (5)	calls	
Apr 22	86	86-19	ERP 12	e of Roche Percee (5)	lt,lt,sev w	
Apr 22	86	86-22	ERP 13	w of Pinto (6)	6t	
Apr 22	86	86-23	ERP 14	Pinto (7)	w	
Apr 29	86	---	ERP 15	Pinto (7)	t,?	
Apr 10	85	85-44	ERP 16	sw of Hirsch (8)	t	
Apr 22	86	86-29	ERP 17	sw of Hirsch (8)	3t	
Apr 11	85	85-55	OGE 02	sw of Oxbow (9)	t	
Apr 23	86	86-33	OGE 04	sw of Oxbow (10)	t	
Apr 11	85	85-57	OGE 03	sw of Oxbow (11)	w,t (pair)	Gray
Apr 23	86	86-40	OGE 06	s of Oxbow (12)	t	Gray
Apr 23	86	86-38	OGE 08	s of Oxbow (13)	t	Gray
Apr 24	86	86-52	OGE 09	sw of Glen Ewen (14)	t	Gray
Apr 12	85	85-65	OGE 11	s of Glen Ewen (15)	t	
Apr 24	86	86-48	OGE 12	s of Glen Ewen (15)	t	Gray
Apr 12	85	85-66,72	OGE 13	s of Glen Ewen (16)	t	
Apr 24	86	86-47	OGE 14	s of Glen Ewen (16)	t	
Apr 12	85	85-73	OGE 15	s of Glen Ewen (17)	t,t (pair)	
Apr 24	86	86-46	OGE 16	s of Glen Ewen (17)	t	Gray?
Apr 24	86	86-45	OGE 17	s of Glen Ewen (18)	t	Red
Apr 24	86	86-44	OGE 18	s of Glen Ewen (19)	t	Red

records, recorded before the split into two species, are cited only as "screech owl". This analysis is not intended to be exhaustive. It does, however, serve to place the Saskatchewan range of the Eastern Screech-Owl into a regional context. Since this is an overview paper, only some American Birds records are referenced, and then only in the text. Figure 2 portrays the Souris River Study Area, and figure 3 portrays the range of the Eastern Screech-Owl at the northwestern extent of its' range in North America. Numbered areas in the discussion refer to locations in figure 3.

Saskatchewan

Godfrey (1966) included the Regina area and parts southeast within the range of the Eastern Screech-Owl but has recently dropped that portion of the range and represented it by a "?" (Godfrey 1986). Godfrey (1966, 1986) also places a "?" in southwestern Saskatchewan. The former range delineation is more appropriate to the present situation. Scott (1983) includes only the extreme southeastern corner of the province and Marshall

(1967), the entire southern portion south of Regina.

The author has collected over 100 Saskatchewan screech-owl records from 1880 to date. These, including the records obtained during the 1985 and 1986 censuses and letter campaign, will be described in detail in a later paper (Adam [n.d.]⁵). To save space, some unpublished sources are cited as Adam [n.d.]⁵.

Southeast.--The core of the Eastern Screech-Owl range in Saskatchewan is the Souris River (1) east of Estevan, with concentrations at Estevan to Roche Percee, Oxbow to Glen Ewen, and at the Saskatchewan / North Dakota border (fig. 2). The modern occurrences correspond to historical references, indicating that there has been a viable population along the Souris River since at least the 1920's. The majority of records are of birds on territory that were censused by the use of tape playbacks. Records away from the river valley probably correspond to the fall and winter dispersal of young birds, or are of adults looking for food. Recent records

from the headwaters of the Souris River (2) indicate that screech-owls occur there occasionally (Adam [n.d.]⁵).

Central.--Pockets of maple woods along Wascana Creek (3) near Regina have supported from zero to three pairs of screech-owls in the recent past (Adam [n.d.]⁵). Such fluctuations are probably typical of a peripheral population. There are also several pre-1961 fall and winter records for the city of Regina (Belcher 1980) and recent records for north of Moose Jaw (3) (eg. AB 33:781-782). The city of Moose Jaw (4) has harboured a territorial owl for the last several years in a pocket of typical maple habitat along the Moose Jaw River. A fledgling extracted from a chimney there in 1979 (AB 34: 172-174) is the only evidence of the breeding of this species in Saskatchewan.

The Qu'Appelle River valley seems ideal for screech-owls in some localities, but only Katepwa (5) has produced confirmed records of territorial owls (Adam [n.d.]⁵; Callin 1980). No records exist for the eastern portion of the valley, although the area has potential for screech-owls.

East.--Generally, screech-owls are absent from the almost treeless prairie north and east of the Souris River (6), although there are some historical records of non-territorial owls (Adam [n.d.]⁵). A few scattered records exist for the area between the Qu'Appelle and Souris rivers, including two historical records of calling birds from the southern edge of Moose Mountain Provincial Park (Adam [n.d.]⁵; Nero and Lein 1971). The maple habitat in this region appears to be rare, and few surveys have been conducted.

Northeast.--Yorkton area (7) records include several non-territorial and one territorial screech-owls, indicating the presence of a small semi-permanent population (Adam [n.d.]⁵; Hjertaas 1986; Houston 1949; Pollock 1986). There are recent records of calling birds from Duck Mountain Provincial Park (8) (Adam [n.d.]⁵; Hatch and Weidl 1981⁶; Soper 1970⁷). A 1979 record of a calling bird from the Porcupine Hills (9) is the most northerly in Saskatchewan (AB 33:872-873).

North.--Two extralimital records (1970's) from the city of Saskatoon (10) indicate the accidental presence of both the western (hypothetical) and eastern species (Adam [n.d.]⁵).

Southwest.--Two areas in southwestern Saskatchewan have produced four screech-owl records, indicating that the species' status is extremely rare and local. Recent screech-owl records from the Frenchman River (11), and Eastend (12) may represent birds which have moved up the Frenchman River from the Milk River in Montana (Adam [n.d.]⁵). The Cypress Hills owl (13) (AB 39:451-452), although not identified to species, is probably an Eastern Screech-Owl which may have moved up the Battle River from the Havre, Montana, area, also on the Milk River.

Manitoba

Southern Manitoba is within the continuous range of the Eastern Screech-Owl according to Godfrey (1986), Marshall (1967) and Scott (1983), although the portrayal of the three ranges differs slightly. Godfrey (1986) suggests that the subspecies O.a. swenki, a pale race with two colour phases, is the bird in southwestern Manitoba, and that it grades into the darker naevius (the widely distributed eastern subspecies) at Winnipeg and Whitemouth. Marshall (1967) considers swenki to be included within maxwelliae. Sources include American Birds reports and CBCs, personal communications, Manitoba Museum of Man and Nature files (specimens and nest records)⁸ (Adam [n.d.]⁵); and published literature.

Southwest.--There are a few scattered records for southwestern Manitoba, ranging from Riding Mountain National Park in the north to Lyleton in the extreme southwest. There are several observations dating from 1972 from the Lyleton area (14), including Knapton's (1979) records of calling birds and flightless young and other similar records from the 1980's. Lyleton is only about 80 km northwest of the Bottineau / Dunseith area of the Turtle Mountains of North Dakota (24) where there have been screech-owl records for years, and also about 60 km due east of a concentration of screech-owls in the southern part of the Souris River in Saskatchewan (1).

Other records come from the Sinclair and Reston area, where a family of screech-owls has hatched annually in the 1980s in or near a park in the latter (15). There are recent winter records from Brandon, Oak Lake and Rivers (16). Riding Mountain National Park (17) is also the site of a rare historical occurrence of a screech-owl (Penak 1985³; Soper 1953), which appears to be Manitoba's most northerly record.

Central.--There are a few scattered observations between southcentral Manitoba (18) and Lake Manitoba (19). The former area (18) includes two 1927 specimens from La Riviere on the Pembina River; a recent specimen from Cypress River; and documented nests from Roland (Copland 1986⁸).

The Winnipeg Area.--Screech-owls appear to be well established in Winnipeg and area (20), the large number of records in no doubt due to the many observers. Specimens exist from Argyle, Dugald, Headingley, and St. Adolph (on the Red River); city parks and other areas are the source of several specimens and nest records (Copland 1986⁸).

The Eastern Forest.--Taylor (1983) describes some historical screech-owl records from Brokenhead and the Whitemouth area (21). There is no evidence that screech-owls are regular breeders in this region of the province.

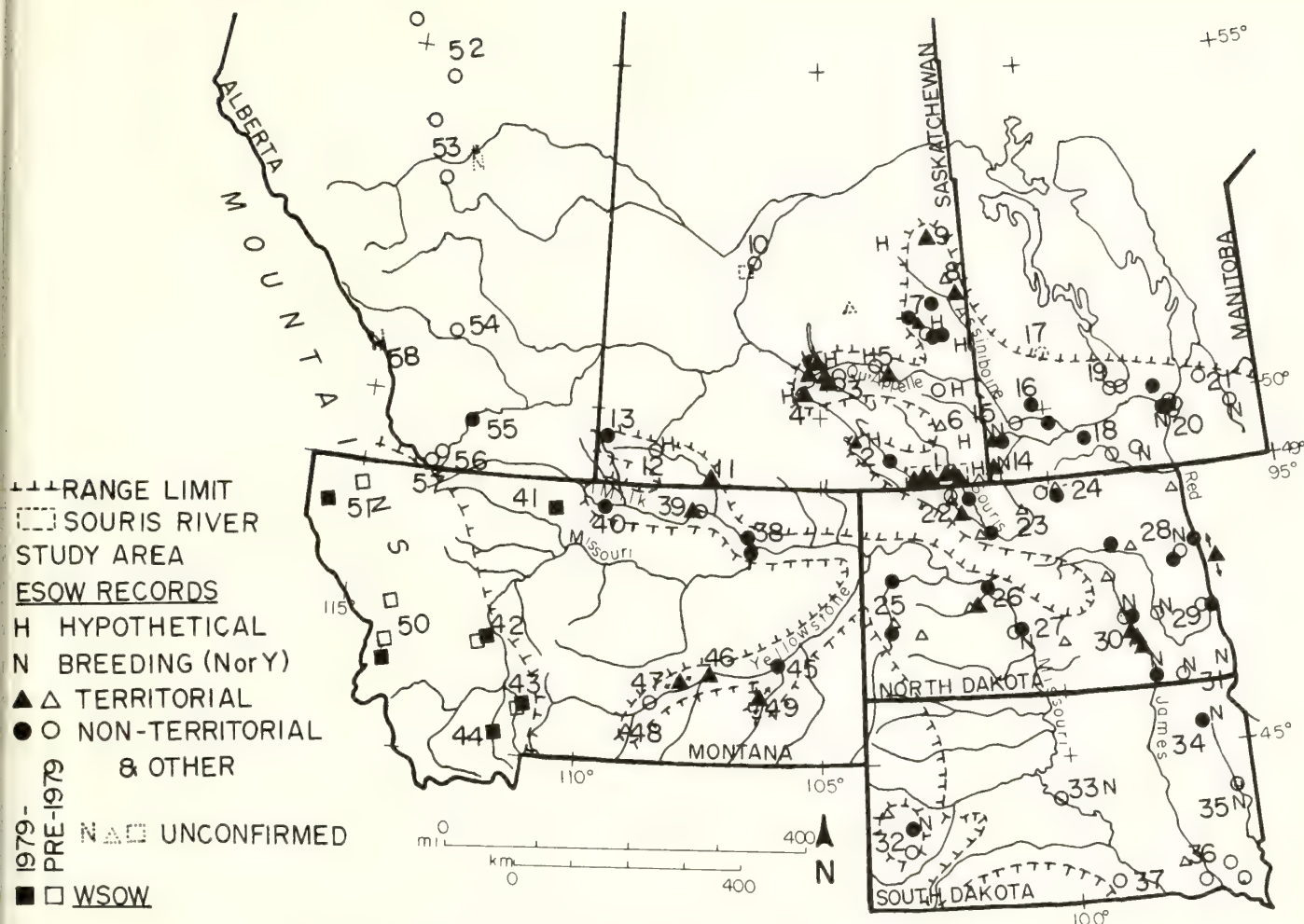


Figure 3.--The range of the Eastern Screech-Owl in Saskatchewan, Manitoba, North Dakota, South Dakota, Montana and Alberta. Numbers refer to locations described in the text.

North Dakota

Marshall (1967) and Scott (1983) include all of North Dakota within the range of the Eastern Screech-Owl. However, Johnsgard (1979) includes only the eastern portion of the state (east of the Missouri River), and the Turtle Mountains. There are many scattered records from the western part of North Dakota whereas the eastern part of the state is within the continuous portion of the screech-owl range. Recent records from *American Birds*, *Audubon Field Notes* and Stewart (1975) were used to update the range in the Dakotas and to compare it with that in Saskatchewan.

The Souris River.--The Des Lacs River, which joins the Souris at Minot, and the western portion of the Souris River are the sites of several records (22). These areas are situated within 100 kilometres of the concentration of screech-owls just over the Saskatchewan - North Dakota border in Saskatchewan. The Des Lacs National Wildlife Refuge (NWR) is the source of several pre-1975

winter screech-owl records (eg. AB 29:461), and the Upper Souris NWR on the Souris River northwest of Minot is the source of three recent winter records (eg. AB 40:879). At Carpio, further to the southeast on the Des Lacs River, a pair of screech-owls with six young was observed in 1979 (AB 33:874-875). Minot is the site of regular CBCs where screech-owls have been recorded since 1978 (eg. 40:878-879). The J. Clark Salyer NWR (23) on the Souris River northeast of Minot is the probable source of several pre-1972 records of territorial males or pairs (Stewart 1975), indicating breeding in this portion of the river. More owls will probably be found along the North Dakota portion of the Souris River if survey efforts are initiated.

The Turtle Mountains.--The Turtle Mountains (24) are an extension of Manitoba's Turtle Mountains and Turtle Mountain Provincial Park, which lies east of Lyleton (14), the site of several screech-owl breeding records. The area is given a disjunct range representation in Johnsgard (1979). The Turtle Mountains are the site of

several pre-1972 records of territorial males or pairs (Stewart 1975). There is a summer record from Bottineau (AFN 23:712-713) and two recent winter records from Dunseith (AB 38:684 and AB 39:677).

The Missouri River.--Western North Dakota has recent winter records from Medora (AB 38:685 and AB 39:678) and the North Unit of Theodore Roosevelt National Park, both on the Little Missouri River (25) (eg. AB 40:879); Garrison Dam on the Missouri River (26) (eg. AB 40:877-878); and Bismarck - Mandan, also on the Missouri River (27) (AB 40:877); and other records from the Beulah/Hazen area on the Knife River (26) (eg. AB 36:866-868). Nesting has also been confirmed from Burleigh and Kidder counties (east of the Bismarck area) (Stewart 1975).

The East.--Eastern North Dakota has screech-owl records centered at Grand Forks (28) (eg. AB 35:612) and Fargo (29) (eg. AB 32:741) on the Red River, well within the continuous Eastern Screech-Owl range. Nests and young have been found in Cass and Barnes counties (29), Stutsman and La Moure counties (30) and Richland county (31) (Stewart 1975). On Feb. 2, 1981, C.A. Faanes recorded responses to taped calls at eighteen locations along the James River between Jamestown and LaMoure (30) (AB 35:311-313). Jamestown is the site of numerous winter records (eg. AB 37:653-654). Lambeth (1986)⁹ estimates that there is more than 1 breeding pair of Eastern Screech-Owls per river-mile along the Red River and its tributaries (28, 29).

South Dakota

Eastern and central South Dakota, and the White River area and Black Hills are included in Johnsgard (1979), while Marshall (1967) and Scott (1983) include the entire state in the breeding range of the Eastern Screech-Owl. Because of the relative lack of information, figure 3 presents the range as given in Johnsgard (1979). Sources used in this summary consist of citations in American Birds and Audubon Field Notes.

The Black Hills (32) contain some records from Rapid City, including nesting records (eg. AFN 22:617-620). Central South Dakota has records from Pierre, on the Missouri River (eg. AB 40:880), and breeding records from Highmore to the east (eg. AB 34:906-907) (33). Other records are from Roberts County (downy young: AB 31:1150-1154) and Waubay National Wildlife Refuge (AB 40:881) in the northeast (34); the Brookings area in the east (35) (AB 32:220-223); Clay, Yankton and Hutchinson counties, and Hurley, in the southeast (36) (eg. AB 34:284-285); and the Burke area in the south-central portion of the state (37) (eg. AB 30:969-972).

Montana

Marshall (1967) and Scott (1983) place the eastern extent of the Western Screech-Owl range

along the Continental Divide of Montana's Rocky Mountains. However, these two authorities differ in portraying the western extent of the Eastern Screech-Owl range. Marshall (1967) shows a line extending due south from the Saskatchewan / Alberta border, while Scott (1983) includes only the Yellowstone River and southeastern Montana. Recent records from American Birds and the status of both kennicottii and asio by latilong in Skaar et al. (1985) were used to summarize the ranges in Montana.

The Milk River.--The Milk River, which joins the Missouri near Fort Peck, has several scattered "screech-owl" records: the Glasgow area (38) (eg. AB 34:284-285); Bowdoin NWR where screech-owls have been seen in nest boxes (39) (AB 33:782-784); and Havre (40), a 1981 winter record (AB 36:684). The Milk River is the probable source of the three recent Saskatchewan records: the Frenchman River (11) and Eastend (12) via the Frenchman River from the Bowdoin / Glasgow / Fort Peck area; and the Cypress Hills (13) via the Battle River from the Havre area. Chester (41), southwest of the Milk River but still within the region, is the site of a Western Screech-Owl identified on a 1982 CBC (AB 37:696). Based on the assumed ranges of both species, the Havre and Chester owls are probably Eastern Screech-Owls and not westerns, unless a diagnostic song was heard.

The Missouri River.--Records for the Missouri are very few, and include Fort Peck (38) (Skaar et al. 1985); and Helena (42) (AB 37:202-204), Bozeman (43) (eg. AB 37:696) and Ennis (44) (AB 37:696), in the Rocky Mountains. Both Bozeman and Ennis are the sites of recent winter records of the Western Screech-Owl.

The Yellowstone River.--The Yellowstone River also supports scattered Eastern Screech-Owls, with records from Miles City (45) (AB 37:312-314); the Hysham area (46), where 10 screech-owls were censused along a ten-mile route (Lambeth 1986)⁹; the Billings Latilong (47), where breeding has been confirmed (Skaar et al. 1985); Joliet (48) (AB 30:87-90); and the Tongue River (49), where census routes have consistently yielded screech-owls (Lambeth 1986)⁹.

The Mountains.--There are several definite Western Screech-Owl records from near the western border of Montana, west of the Continental Divide (50, 51) (eg. AB 38:727). These will not be considered in this paper.

Alberta

Although I have not been able to confirm any of the Alberta records (Salt and Salt 1976; Penak 1985³), most are probably Eastern Screech-Owls except possibly those from Waterton Park. The most northerly records are from Flatbush and Kinuso in the Swan Hills region (52). There also have been records from the Edmonton area (53), including Belvedere, Eilerslie and Pigeon Lake. There is also a 1950's record from east of Calgary

(54) and one from the Lethbridge area (55). The most southerly records are from Cardston (56) and Waterton Lakes National Park (57). An 1897 breeding record from Banff (58) is the earliest record.

The Waterton birds may have been extralimital Western Screech-Owls, but they are undoubtedly unconfirmable sight records. The southern birds may have moved in from Montana and Saskatchewan. The Banff bird may have been a Western Screech-Owl. The Eastern Screech-Owl should probably be listed as accidental for Alberta.

CONCLUSIONS

Investigations into the range and status of the Eastern Screech-Owl in Saskatchewan have shed some light on the situation in Manitoba, North Dakota and Montana. South Dakota and Alberta have not been examined as closely due to the relative lack of data. The range delineation (fig. 3) is still preliminary in nature, pending further documentation. The situation is complicated by the fact that *Otus kennicottii* was split from *Otus asio* only in 1983 (AOU 1983). Earlier records are thus not directly separable.

It is clear that the Souris River in southeastern Saskatchewan is the centre of the range in that province, with peripheral areas such as Moose Jaw, Regina, Yorkton and Duck Mountain having low and occasional populations. Some isolated records indicate that owls have dispersed in winter from the Souris River, or have moved along the valley to other areas. Similar movements may account for the presence of owls along the Qu'Appelle and the Assiniboine rivers

(Yorkton area, Duck Mountain). However, the presence of owls in Regina and Moose Jaw may be better explained by owls moving across the intervening space between the Souris system and the Moose Jaw River and Wascana Creek.

Western Screech-Owls inhabit riparian habitat within the mountains of Montana, and Eastern Screech-Owls similar areas in the central plains (AOU 1983; Scott 1983). However, the northcentral portion of Montana appears to be in a state of flux. The preliminary range in this paper indicates that *asio* is gradually spreading westwards along the Yellowstone, Missouri and Milk rivers, and into Saskatchewan via the Frenchman and Battle rivers.

The situation in Montana and southern Alberta shows that the ranges of the two species are not yet set. This brings to light some interesting questions. The Chester and possibly the Havre owls may be *kennicottii*. Did they move east out of the mountains of Montana, were they misidentified, or were they unidentified *asio*? How far is *asio* moving west? Is *kennicottii* moving east, and how far? Are the Alberta owls, most of which are old records, *asio*, or are some of them *kennicottii*? Further studies and data collection may shed some light on this situation.

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Effects of Environmental Variables on Responses of Eastern Screech Owls to Playback¹

Thomas W. Carpenter²

Abstract.--Seventeen woodlots were censused for Eastern Screech-Owls using the playback technique from January of 1983 to August of 1984 to examine the effects of cloud cover, temperature, season, wind, and the lunar cycle on playback responses. Cloud cover, the lunar cycle, and winds under 25 kmph had no significant effects on the ability to find Eastern Screech-Owls with playback. The mean response latency was significantly less in winter than spring. Fewer birds were found when temperatures were below -12 °C.

INTRODUCTION

Many investigators have used playback in studies of the Eastern Screech-Owl, *Otus asio* (Casner 1974, Nowicki 1974, Cink 1975, Beatty 1977, Ellison 1980, Smith and Walsh 1981, Andrews et. al. 1982, Lynch and Smith 1984, Muttter et. al. 1984). Despite such widespread use, the influence of environmental factors on the results of playback studies has received little attention. In this study I examined whether the lunar cycle, season, cloud cover, temperature, and moderate (9-24 kmph) versus light (0-8 kmph) winds had any significant effects on the responses of the Eastern Screech-Owl to playback.

METHODS

Using playback, I censused 17 south-east Wisconsin woodlots for Eastern Screech-Owls from 16 January 1983 to 20 August 1984. Each woodlot was censused at 3 to 6 wk intervals. All woodlots were known to have at least one resident Eastern Screech-Owl. During each census attempt I recorded the day of the lunar cycle, the temperature in °C, wind speed

in kmph and the percent of the sky covered by clouds (estimated to the nearest 5%). Response latency (the length of time from the initiation of playback to detection of a bird) was also recorded. No censusing was done when winds exceeded 25 kmph or during heavy precipitation as other investigators have shown these conditions to severely restrict the ability to detect owls (Simpson 1972, Siminski 1976, Whisler and Horn 1977, Forsman 1983). Censusing was usually carried out between 0200 and 0500 and all censusing was done after 2000. Time of censusing between these limits was found to have no significant effect on the results of playback (Carpenter 1985).

The recording used in playback was taken from the Peterson record series A Field Guide to Bird Songs and consisted of a 12 min sequence: 3 min of calling, 1 min of silence, 3 min of calling, 1 min of silence, 3 min of calling and a final min of silence. The spacing between calls in the 3 min segments was 5 s. The recording was played from a Uher 4000 model tape recorder and amplified with a Nagra DH amplifier-speaker to a level of 92 dB. When birds were detected, playback was terminated. Otherwise, the 12 min playback procedure was completed. If birds were not detected after this it was assumed they would not respond.

The G test (Sokal and Rohlf 1983) was used to test for a relationship between each variable and the response rate to playback. One-way ANOVA's were used to test for any influence of each variable on mean response latency. The Tukey-Kramer method was used to deter-

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mine significant differences between means if a relationship was shown by the one-way ANOVA. Results were considered significant if $P < .05$.

Seasons used for this study were defined on the basis of the timing of significant events in this species annual cycle in southeast Wisconsin are as follows: winter (16 Dec to 15 Mar), spring (16 Mar to 15 Jun), summer (16 Jun to 15 Sept) and fall (16 Sept to 15 Dec).

RESULTS AND DISCUSSION

Temperatures less than -12°C appeared to have an inhibitory effect on response rate (1 response out of 9 census attempts) but there were insufficient data to demonstrate this statistically (table 1). Casner (1974) found that "bitterly cold" temperatures diminished success and Smith and McKay (1984) noted there was an increase with warmer temperatures in the numbers of Eastern Screech-Owls reported on Christmas Bird Counts. Winter temperatures well below normal should be avoided as they appear to affect significantly the results of playback with this species.

I did not observe any relationship between the phase of the moon and response latency ($F = 1.13$, $df = 2$, 88, NS). Also, response rate to playback was not affected by the lunar cycle ($G = 0.82$, 2 df , NS). Johnson et. al. (1979, 1981) found Western Screech-Owls were most readily located with playback on nights



Figure 1.--Gray phase Eastern Screech-Owl Photograph by Lee A. Carpenter.

Table 1.--The effect of temperature on response rates.

Temperature	No. of census attempts with a response	No. of census attempts without a response	Totals
-19 to -7°C ¹	20	22	42
-6 to -1°C	5	8	13
0 to 5°C	22	21	43
6 to 11°C	15	13	28
12 to 17°C	21	10	31
18 to 25°C	<u>14</u>	<u>15</u>	<u>29</u>
Totals	97	89	186

$$G = 4.64, df = 5, P > .05$$

¹When temperatures were -19 to -12°C one response was obtained out of 9 census attempts. This data had to be combined with the next temperature category (-11 to -7°C) to satisfy the requirements for the statistical test used.

with a bright waxing moon.

I found no significant differences in response rates ($G = 0.50$, $df = 1$, NS) or response latency ($F = 0.23$, $df = 1$, 89, NS) for light (0-8 kmph) versus moderate (9-24 kmph) winds. Siminski (1976) and Whisler and Horn (1977) found wind to have a negative effect on playback success in locating Great Horned and Spotted Owls.

Season did not affect the rate of response ($G = 2.04$, $df = 3$, NS). However, there were seasonal differences in the numbers of owls detected per successful response. More birds were detected per successful response during July and August when young birds frequently responded. This late summer increase in numbers has been previously reported by Allaire and Landrum (1975) and Lynch and Smith (1984). Also, pairs of birds (as opposed to single birds) appear to respond most often during winter (table 2). Season also had an effect on response latency. The mean response latency for winter was significantly different from that of spring with birds responding most rapidly in winter and taking the longest to respond during spring (table 3).

Cloud cover did not affect either response latency ($F = 0.56$, $df = 3$, 87, NS) or the rate of response ($G = 1.86$, $df = 3$, NS).

In summary, the environmental factors

Table 2.--Single bird responses and responses of pairs of Eastern Screech-Owls with respect to season.¹

Season	No. of times only a single bird responded	No. of times a pair responded	Totals
winter	14	7	21
spring	18	3	21
summer	14	4	18
fall	13	1	14
Totals	59	15	74

¹The table only includes data from the 12 woodlots where pairs were present.

I studied had little effect on response to playback. Extremely low winter temperatures do seem to inhibit responses. The only variable examined that significantly affected response latency was season. My findings further reinforce playback as an effective method for studying Eastern Screech-Owls.

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Table 3.--The effect of season on mean response latency.

Mean response latency in min					
winter	fall	summer	spring	F	df
3.23 ± 2.02	3.90 ± 2.95	5.32 ± 3.41	5.65 ± 2.83	3.65*	3, 87

* significant seasonal effect (P < .05; one-way ANOVA)

Means connected by the same line do not differ significantly (P > .05; Tukey-Kramer method)

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Current Status and Habitat Associations of Forest Owls in Western Montana¹

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Abstract. Nine species of owls nest in the forests of western Montana. Except for the Great Horned Owl, little is known about the other species. Only one Flammulated Owl nest has been reported in Montana. Western Screech Owls are mostly associated with riparian zones. Barred and Great Gray Owl nest site information is minimal. Boreal Owls are believed to be associated with old-growth spruce/fir forests above 1,500 m elevation. Nesting Saw-whet Owls seem to be associated with old, large, ponderosa pine snags. There is currently little data available for resource managers to make sound land-use decisions. Surveys must be established to gain basic habitat preference information for the species group.

INTRODUCTION

Little is known about the status and the habitat requirements for forest owls in western Montana. Except for the Great Horned Owl (*Bubo virginianus*), which exists in almost all habitats throughout the State, resource managers have little information available on which to make sound land-use decisions that will maintain viable populations of forest owls. Even the most basic information regarding the potential impacts of timber harvest or firewood cutting on this species group is lacking. The purpose of this paper is to centralize the current status and present preliminary information on habitat distribution of these owls for resource managers, researchers, and interested persons in western Montana. In addition we ask, what are the responsibilities of United States Forest Service to this species group, and briefly comment on two management strategies often implemented.

Further, we provide general census information guidelines (Tables 1, 2, and 3) and data sheets (Appendices 1, 2, and 3) for western Montana should the need or interest occur.

Before any research or management goals can begin, we feel it is essential to provide a foundation to work from. The following species accounts, however minimal, are state-of-the-art information for eight forest owls in western Montana. We define western Montana as the portion of the Rocky Mountains from the Idaho/Montana border east to our arbitrary line (Fig. 1).

We have not included the Great Horned Owl because of its wide distribution and diverse habitat association in western Montana or the Eastern Screech Owl (*Otus asio*) because this species has yet to be found in the area covered by this map.

SPECIES ACCOUNTS

The following is a summary of information collected thus far including nest data collected by other individuals.

FLAMMULATED OWL (*Otus flammeolus*) - Skaar et al. (1985) list five records--all occurring in western Montana. More recently, Holt, et al. (submitted for publication) has added six recent records, including the first nest record for Montana. The Flammulated Owl is a cavity-nesting owl strongly associated with old-growth ponderosa pine (*Pinus ponderosa*) (Bull and Anderson 1978; Linkhart 1984; Reynolds and Linkhart 1984). In

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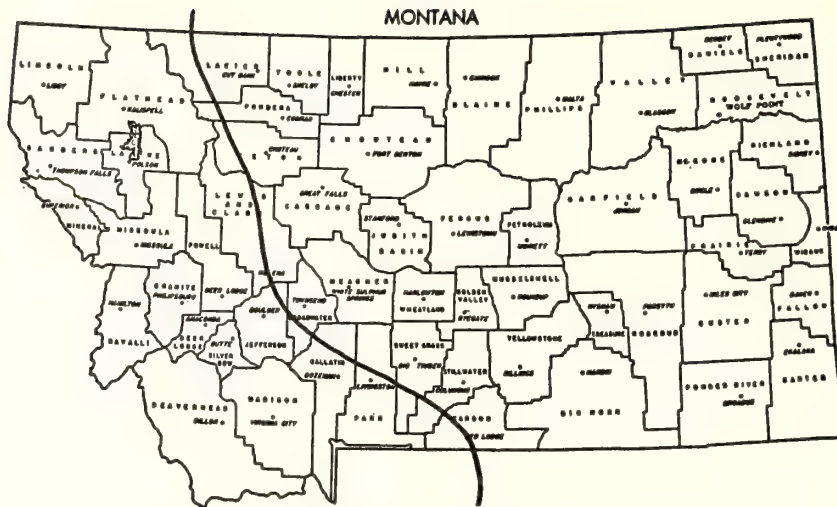


Figure 1. Area left of line delineated as Western Montana

Montana, the only vocalizing adult Flammulated Owls and present nest records are associated with old-growth ponderosa pine habitat (Holt, et al., submitted for publication). In the more southwestern limits of its range, ponderosa pine and Jeffrey pine (*Pinus jeffreyi*) were also used (Winter 1974). Marcot (1980) and Webb (1982), however, indicate an association of Flammulated Owls with mature California black oak (*Quercus kelloggii*) and quaking aspen (*Populus tremuloides*), respectively.

WESTERN SCREECH-OWL (*Otus kennicottii*) - Skaar (1975, 1980) listed numerous breeding and probable breeding locations for the Screech Owl (*Otus asis*) throughout western Montana. Since the recent split of the Screech Owl into two species, Western Screech Owl and Eastern Screech Owl (AOU 1983), problems concerning the distribution of these two species in Montana are being investigated. Of nine specimens from western Montana (Fig. 1), examined by Philip L. Wright, University of Montana Zoology Department, Missoula, Montana, all have been identified as the Western Screech Owl. This is the most current information we have to date. The only nest sites we could locate were: one in a natural cavity in a black cottonwood (*Populus trichocarpa*); one in a nest box attached to a black cottonwood; and one in a pileated woodpecker (*Dryocopus pileatus*) hole in a quaking aspen (B. R. McClelland, pers. comm.). Several observers have reported fledglings along cottonwood habitats surrounding Missoula, Montana. Vocalizing adults have been heard along major streams and rivers from 1976 to present (W. Kerling, pers. comm.) This is undoubtedly a more common species closely associated with riparian habitats. These habitats represent a small fraction of western Montana's forest zones and should be looked at more closely. Efforts to locate (by vocalization) forest owls throughout western Montana in 1984 and 1986 failed to elicit any Western Screech Owl responses in coniferous

forests at elevations ranging from 600 to 2,400 m in elevation, despite seven other owl species responding (Escano 1984; Holt 1986). However, these owls are occasionally observed in mixed coniferous forests away from riparian areas.

NORTHERN PYGMY-OWL (*Glaucidium gnoma*) - The Pygmy Owl is a common resident throughout the mountains of western Montana. Because of this owl's diurnal activity throughout the winter, it is commonly seen at bird feeders, on power lines along the road, or chasing flocks of wintering passerines. It is rarely seen, however, during the nesting season when it becomes more secretive and crepuscular. There is almost nothing known of its habitat requirements in North America (Norton and Holt 1982, Holt and Norton 1986). Observations and vocalization in western Montana indicate a preference of Pygmy Owls for mixed/fir or spruce/fir forests during the breeding season (D. Holt, unpub. data), although others have reported nests in old woodpecker holes in poplar and aspen trees (*Populus spp.*) in California and Oregon (Bendire 1888), western larch (*Larix occidentalis*) in Oregon (Munroe 1919), a natural cavity in a black oak in California (Holman 1926), and a woodpecker hole in an aspen tree in Oregon (Brady 1930).

BARRED OWL (*Strix varia*) - The Barred Owl appears to be a recent addition to Montana avifauna. However, Saunders (1921) reported two Barred Owls collected near Billings, Montana; but the specimens have never been located and there is some question as to their authenticity (P. D. Skaar, personal records). Early reports of Spotted Owls (*Strix occidentalis*) (Weydemeyer 1927, Hoffman et al. 1959, Hand 1969) in northwestern Montana may also be questionable (Wright 1976) and could represent earlier Barred Owl records. The first accurate records for a Barred Owl in Montana appeared on July 30, 1966 in Glacier National Park (Glacier National Park Bird Record Cards). Shea (1974) summarizes the

recent range expansion in western Montana, which seem to center around northwestern Montana. The first verified nest was reported on May 29, 1976 (Rogers 1976). Taylor and Forsman (1976) and Boxall and Stephney (1982) discuss range expansion of the Barred Owl and permanent residence in western North America and Alberta, respectively.

Despite 20 years of possible range expansion in Montana, few nests have been reported (Rogers 1976, 1979, 1982) and habitat associations are just beginning to be identified. Over the last 5 years near Libby, Montana, three Barred Owl nesting territories have been located. All were associated with mixed species of old-growth forest between 900 to 1,200 m in elevation; however, no actual nests have been found (A. Bratkovich, pers. comm.). In 1985, vocalizing adults and a probable nest site was located near Rainy Lake in the upper Clearwater River drainage of Montana. The nest was in a stand of scattered old-growth western larch (M. Hillis, pers. comm.). One Barred Owl nest reported, was found in the broken top of a live western larch approximately 1,200 m in elevation (R. Kuennen, pers. comm.). Over the past 10 years in Glacier National Park, four Barred Owl nests were found in broken-top old-growth western larch trees, approximately 1,000 m in elevation (B. R. McClelland, pers. comm.). Also, vocalizing adult Barred Owls during the breeding season have been associated with old-growth western larch stands in the Rattlesnake Wilderness Area, Missoula, Montana, from 1976 to present (W. Kerling, pers. comm.). Current surveys (D. Holt, unpubl. data) have located Barred Owls during the nesting season from 900 to 1,800 m elevation in riparian (one record), mixed larch, and lodgepole pine (*Pinus contorta*) habitats.

GREAT GRAY OWL (*Strix nebulosa*) - Skaar et al. (1985) list this owl as a fairly common resident throughout western Montana. However, there are only ten known nest records (Weydemeyer 1932; Hand 1969; Rogers 1972, 1975, 1976, 1977, 1979, 1982; Skaar pers. records) that we could locate, despite numerous sightings and suspected nesting areas. Most of these, however, were east of the Continental Divide. Great Gray Owls are typically associated with lodgepole pine/wet meadow ecotones east of the Continental Divide in Montana (S. Gniadek, pers. comm.). Escano (1984) reported Great Gray Owls occurring in lodgepole pine/wet meadow complexes between 1,500 to 2,300 m in elevation only east of the Continental Divide, despite surveys on both sides. West of the Continental Divide, J. Foote (pers. comm.) reported Great Gray Owls probably nesting in the last 4 to 6 consecutive years in spruce bogs near Ovando, Montana. In addition, D. Holt (unpubl. data) located Great Gray Owls in spruce/fir bogs approximately 1,800 m in elevation in western Montana. Nero (1980) also reported Great Gray Owls using nests in spruce bogs from Manitoba, Canada. There are enough sightings to indicate that this owl occurs regularly west of the Continental Divide in Montana, but surveys are

needed to locate breeding territories and nest trees.

LONG-EARED OWL (*Asio otus*) - While this is one of the more common owls in the State (Skaar et al., 1985), information concerning forest habitat preferences is lacking. Nesting of this species in old magpie (*Pica pica*) or American crow (*Corvus brachyrhynchos*) nests in dense deciduous vegetation in shrubsteppe desert is well documented (Marks 1986). Similar nest sites have been recorded in eastern (S. Gniadek, pers. comm.) and western (D. Holt, unpubl. data) Montana. They are reported to nest in woodlands bordered by meadows in Europe (Mikkola 1983). However, there seems to be a scarcity of information concerning habitat preferences in the coniferous forests of western Montana. Vocalizing adults have been heard in mixed Douglas-fir (*Pseudotsuga menziesii*) stands near Missoula, Montana (D. Holt, unpubl. data), and a stick nest was found in a lodgepole pine tree in Glacier National Park, Montana in July 1985 (Glacier Park Bird Record Cards). But, to what extent is this really a forest owl?

BOREAL OWL (*Aegolius funereus*) - Skaar et al., 1985) list 16 verified records for Montana. Though no nests have been located, three juveniles were observed in Glacier National Park by Dave Shea in July 1973. This constitutes the only evidence of breeding for the State. More recently, Escano (1984) and Holt (1986) have conducted specific surveys to locate Boreal Owls in western Montana. An additional specimen record (Holt et al., in press) and a sighting record (T. Ryan, pers. comm.) were also reported in 1986. Thus far, survey results indicate that Boreal Owls in western Montana prefer mature old-growth spruce/fir forests greater than 1,500 m in elevation, though east of the Continental Divide, some survey results were associated with lodgepole pine/wet meadow habitat. Hayward and Garton (1983) and Palmer and Ryder (1986) summarized the first nesting and documented nesting records for Boreal Owls in Idaho and Colorado, respectively. Status and distribution of this owl are slowly coming to light now that surveys to locate them are being conducted in the Rocky Mountain states.

SAW-WHET OWL (*Aegolius acadicus*) - Little information exists in the literature concerning Saw-whet Owls in western Montana. It appears to be a fairly common owl with wide distribution throughout the State (Skaar et al., 1985). Though generally associated with coniferous forests in Montana, Saw-whet Owls have also been located along cottonwood habitats (Youman, et al., 1981; W. Heron, pers. comm.). Of nine nest sites in western Montana from which we are familiar, seven were in dead ponderosa pine snags (D. Holt, unpubl. data), one was in a dead western larch snag (J. Kipphut pers. comm.), and one probable nest was also in a western larch snag (B. R. McClelland, pers. comm.). Two additional nesting territories located in 1986 were associated with mixed ponderosa pine/Douglas-fir habitat (D. Holt, unpubl. data).

SUMMARY OF SPECIES ACCOUNTS

We know very little about habitat requirements for most forest owls of western Montana. We are sure that there may be more information available for several of the species mentioned. Unfortunately, if it is not in the literature or locally reported, it is difficult to find. Five of the eight owl species (Flammulated, Western Screech, Northern Pygmy, Boreal, and Saw-whet) are dependent on tree cavities, either natural or excavated, for nest sites. The Barred and Great Gray Owls either nest in large broken-top snags or large stick nests made by other birds. Long-eared Owls nest in stick nests made by other birds. Seven of the eight species are directly associated to snags and mature or old-growth trees for nest sites. The Western Screech Owl is mostly associated with riparian habitats, which represent a small fraction of western Montana's forest zones. Threats to this habitat could have a great effect on this owl.

WHAT ARE THE RESPONSIBILITIES OF THE FOREST SERVICE?

Do forest management plans provide adequate habitats to maintain viable populations of western Montana's forest owls? Without baseline surveys to locate nesting areas, or more adequate habitat use data, there is inadequate information to answer this question.

With the exception of the Spotted Owl (*Strix occidentalis*), the U. S. Forest Service has not given much emphasis to owl management. This is contrary to the National Forest Management Act of 1976 (NFMA) which mandates that all wildlife species be managed for viable populations. However, with over 500 vertebrate species this would be difficult for any organization. Recognizing the absence of detailed information on owl habitat, the apparent association of owls with snags, mature, and old-growth timber (both rapidly declining), it seems inconsistent that the U. S. Forest Service has placed little emphasis on owl management. One might conclude that the agency's painful experiences with the Spotted Owl in Oregon and Washington have evolved into a "hear no evil, see no evil" approach for other forest owls as well. Fortunately, that attitude may be changing. Some positive signs of that change include: 1) adoption of a Montana sensitive species list that includes two owls--the Great Gray and Boreal; and 2) a commitment to fund intensive inventories for several sensitive species each year. Unfortunately, no species of owls were selected for inventory in 1987.

We suggest an approach to protecting Montana's forest owl populations to include the following steps:

1. An inventory of owl nesting distribution;

2. Cooperation with researchers to define nest-stand selection, territory size, prey base, and population status; and
3. Development of a management strategy for maintaining viable populations for each forest owl species into individual Forest Plans.

The above three steps would allow the U. S. Forest Service to appropriately modify timber harvest and firewood activities in a way that guarantees population viability for forest owls.

"INDICATOR" SPECIES

Using indicator species to indicate effects of management on a variety of species is a commonly used concept. For instance, using the Pileated Woodpecker in western Montana as an indicator for species dependent on old-growth larch-fir forests is "the key to retaining a complete community of hole-nesting birds" (McClelland 1977). For some snag dependent owls, such as the Flammulated, Western Screech, Barred, and Saw-whet, the Pileated Woodpecker may be a useful key. However, this may not help the Northern Pygmy, Great Gray, Long-eared, and Boreal Owls, which appear to be dependent on different habitats. Also, indicator species used in one area may not be applicable to another area. Without basic knowledge of what owls occur in which habitats, how can an indicator species be useful for the species group?

ARTIFICIAL NEST SITES

Artificial nest sites have been used to either manage, protect, or increase wildlife populations. Many of these programs have been successful to help reestablish certain species or gain certain biological information. But to introduce artificial nest sites for convenience or to increase populations not in jeopardy is of questionable value. This turns into single species or group species management, which undoubtedly effects other species of the community. If artificial nest sites are needed temporarily to gather some important information, they should be used temporarily and then removed. For some species, artificial nests may be needed, but to use this tool for managing forest owls in lieu of an active habitat research and management program is unwise. We state this obvious point to challenge the inevitable "quick fix" philosophy that federal agencies or industry groups utilize which often implies that many wildlife problems can be solved with a bird box. Artificial nest sites should be used only where and when it is the last alternative to maintain or reestablish a population in jeopardy. Only habitats that a given species is known to nest in should be influenced. And, when planning such projects, we should seek to approximate the levels of viable

populations that may have been found in other studies of natural populations.

If we go beyond this, then we become like game managers, producing the animals we like best and ignoring the overall continuity of natural community.

CONCLUSION

We have tried to emphasize the lack of information on forest owls in western Montana and the immediate need for baseline surveys. Many of the species may be dependent on snags, mature, or old-growth timber for nest sites. Indicator species currently used to measure ecosystem health may not work for all the owls mentioned. Artificial nest sites should not replace an ecosystem's approach to owl management. It's time to create a strong research and management strategy designed to meet the habitat needs of these owls. The National Forests must lead the way.

Two unfortunate examples help illustrate the need for more information. In March 1986, a Boreal Owl nest territory was located in a mature spruce/fir stand west of Missoula. Later that spring a logging company moved into the area and began operations (Holt 1986). While this provides an opportunity to monitor the effect of logging disturbance on the owls, it is doubtful whether the disturbance-related data will be worth the potential loss of the nest territory. In July 1985, north of Missoula, a firewood cutter felled the first documented nest site for Flammulated Owls in Montana (Holt et al., submitted for publication).

In the case of the Boreal Owl, this was a known nest territory, previously surveyed in 1984 and 1985. While the timber in the area had already been sold to a contractor, could not some contract modification been made to protect the nest stand? The answer, of course, is "yes" if the Forest Service had had an owl management strategy or program to rely on. Regarding the Flammulated Owls, at least the woodcutter reported the incident. This raises another significant question which is, are firewood cutting guidelines and dissemination of information adequate to maintain snags along forest roads?

These are standard old-growth questions, which in the immediate past were most often associated with woodpeckers. Beebe (1974) and McClelland (1977) thoroughly address these issues. Further, Fischer and McClelland (1983) list over 1,700 references pertaining to cavity nesting birds.

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The following tables and appendices for western Montana include: Census Techniques Used (Table 1); Approximate Timeframes and Habitat to Begin Censuses (Table 2); Types of Nests Used and Probably Most Important Trees for Nesting (Table 3); Forest Owl Survey Records (Appendix 1); Roost Site Records (Appendix 2); and Nest Record Sheets (Appendix 3). All sheets can and should be used or modified to meet the needs of the investigator.

TABLE 1

CENSUS TECHNIQUES GUIDELINES FOR WESTERN MONTANA

1. Calling during the nesting season--vocalize or use tape recorder--listen for a few moments before you begin.
2. Initiate calling of the smaller owls first, otherwise calls of the larger owls may intimidate the smaller owls, and they may not respond.
3. Distance between stops is up to the caller, however, a good rule-of-thumb is to use shorter intervals for smaller owls and longer intervals for larger owls.
4. Because routes can run several miles, we suggest calling for approximately 4 to 6 minutes at each stop. Listen 1 to 2 minutes, play the call for 1 minute, listen for 1 to 2 minutes, repeat.

5. Whether you have made contact or not, record your positive/negative success and effort expended on a data sheet. Include species, type of call, date, time, weather, temperature, cloud cover, phase of moon, elevation, habitat, approximate distance to owl, and any other information you wish to include or observations made.
6. At some point back at camp, home, office, be specific about county, drainage, legal description.
7. If nest is found, provide some type of nest record sheet with nest site parameters.
8. Other

TABLE 2

RELATIVE DATES AT WHICH POTENTIALLY
BREEDING OWLS SHOULD BE MOST VOCAL
IN WESTERN MONTANA

Species	Survey Dates	General Habitat
Flammulated Owl	May-June	Mature Ponderosa Pine
Western Screech Owl	Feb.-Early April	Mature Riparian Areas
Northern Pygmy-Owl	Early April-May	Mixed Douglas-fir
Barred Owl	March-April	Mature Western Larch/Douglas-fir
Great Gray Owl	March-April	Spruce/Fir Bog or Lodgepole Pine/Wet Meadows
Long-Eared Owl	March-April	Mixed Ponderosa Pine/Douglas-fir or Lodgepole Pine
Boreal Owl	Feb.-Early April	Mature Spruce/fir
Saw-Whet Owl	Mid-Feb.-April	Mixed Ponderosa Pine

TABLE 3

TYPE OF NEST SUBSTRATE PROBABLY USED AND
PROBABLE MOST IMPORTANT NEST TREES

Owl Species	Nest Site Substrates			Nest Tree
	Cavity	Broken Tops	Stick	
Flammulated Owl	x			Ponderosa Pine/Western Larch
Western Screech-Owl	x			Black Cottonwood/Aspen
Northern Pygmy-Owl	x			Douglas-fir/Ponderosa Pine
Barred Owl	x	x	x	Western Larch
Great Gray Owl		x	x	?
Long-Eared Owl			x	?
Boreal Owl	x			Spruce/Sub-alpine Fir
Saw-Whet Owl	x			Ponderosa Pine/Western Larch

NOTE: Many species may call any time of the year, day, or night. These survey suggestions represent the onset of owl breeding season in western Montana.

APPENDIX 1

FOREST OWL SURVEY RECORDS IN WESTERN MONTANA

Species _____ No. _____ Date _____

State _____ County _____ Area _____

Legal Description T. __, R. __, Sec. __, 1/4 Sec. __,

1/4 1/4 Sec. __ (if available)

Direction to Site (Landmarks) _____

General Habitat Description (i.e., old-growth
spruce/fir greater than 20 ft.) Nest __Y__N

	Survey Responses/Night:
Moon Phase _____	Time Start _____
Elevation _____	Unsolicited Calling _____
Weather _____	Solicited Response _____
(Cldy, Clear) _____	Time End _____
Wind (0,1,2,3) _____	No. Calling Stations _____
Temperature _____	No. Habitat Surveyed _____
Aspect _____	Riparian/Deciduous _____
	Black Cottonwood BC _____
Distance to: _____	Aspen AS _____
	Other _____
Water _____	Coniferous _____
Road _____	Douglas-fir DF _____
(highway/ logging) _____	Ponderosa Pine PP _____
Meadow _____	Western Larch WL _____
Clearcut _____	Lodgepole Pine LP _____
Bog _____	Englemann Spruce ES _____
Other _____	Subalpine Fir SF _____
	Other _____

APPENDIX 2

ROOST SITE RECORDS

Species _____ No. _____

Date _____ Season _____

Legal Description T. __, R. __, Sec. __, 1/4 Sec. __,

1/4 1/4 Sec. __

General Habitat Description _____

Substrate _____	Distance to: _____
Substrate Species _____	Road _____
Roost Height _____	Water _____
DBH (if) _____	Habitation _____
Canopy Cover _____	Open Habitat _____
Slope _____	
Other: _____	Other: _____

APPENDIX 3

NEST RECORD SHEET

Species _____ Nest Name _____ Date _____

Nest Located __Y__N Evidence of Breeding _____

State _____ County _____ Area _____

Legal Description T. __, R. __, Sec. __, 1/4 Sec. __

1/4 1/4 Sec. __

Nest Substrate:

Nest Variables:

Bare Ground _____	Substrate Species (if) _____
Ground _____	Nest Dimension _____
Vegetation _____	Surrounding Vegetation _____
Shrub/Bush _____	Height of Nest _____
Tree (Cavity) _____	Height of Tree _____
Tree (Stick) _____	Height of Cliff _____
Cliff (Cavity) _____	Cavity Dimension _____
Cliff (Ledge) _____	Burrow Dimension _____
Cliff (Stick) _____	Primary Excavator _____
Burrow _____	DBH (diameter at _____
Other _____	breadth/height) _____
	Slope _____
	Canopy _____
	Aspect _____
	Other _____

Distance to:

Road (major, secondary, logging) _____
 Water (river, creek, lake, bog) _____
 Open Habitat (meadow, clearcut, _____
 pasture, grasslands, agriculture) _____
 Other: _____

Potential Disturbance Factors _____

Prey Collection Dates _____

Notes _____

Other Information _____

People Power: Help for the Owl Bander¹

C. Stuart Houston²

Abstract.--A large-scale Great Horned Owl banding program in Saskatchewan evolved because of help available each year from: 1) a relatively constant number of interested farmers who have located and directed me to about 1200 active nests; 2) an ever-changing group of young men who have volunteered to help climb trees and band the young.

INTRODUCTION

My owl studies began innocently from random banding of any bird at hand, including 15 Great Horned Owls, Bubo virginianus, during my first 15 years of banding. Of two recoveries, one was from Bluffton, Minnesota, 450 miles to the southeast, an unusual movement for a year-round resident. This encouraged me to band more owls (Houston 1978).

My efforts near Yorkton, Saskatchewan, were first aided by Bill Horseman, a 15-year-old trapper and birdwatcher, who located 5 nests in 1958 and 23 in 1959. In 1960, I had a weekly birdwatching program on CKOS Television, to promote the Peterson bird cards in Brooke Bond tea and coffee. Peterson's Field Guides were offered to those finding the most owl nests. The results exceeded my expectations when three winning pairs of farm lads found 20, 16 and 10 successful nests, respectively; 150 flightless young were banded that May.

NEST FINDERS

After moving to Saskatoon and completing my training in radiology, I several times placed a request in Doug Gilroy's nature column in the Western Producer, a farm newspaper with 160,000 circulation, asking Saskatchewan farmers to notify me of owl nest locations. This produced responses from a select group of observant, interested and helpful farmers, most of whom have been finding nests for me ever since. Schoolteacher Bryan

Isinger stimulated his pupil, Rosemary Nemeth to find owl nests near Yellow Creek. Peter Boychuk and Maurice Mareschal, teachers in the nearby villages of Crystal Springs and Yellow Creek, soon enlisted their students to find owl nests as well. Most of the successful nest finders listen for the location of owls hooting on their land and watch all large nests seen during farm work and local travel in March and April, before the leaves come out. Leif Nordal searches by ski-doo and Ed Brockmeyer on cross-country skis. Permission is obtained from their neighbors before our banding visit. Three farmers have located 100 successful nests and another six have found 40 or more (Table 1).

Table 1.--Great Horned Owl nest finders, 1968-1986

Leif Nordal, Bill Cochrane at Bulyea	111 nests
Pete Hill at Duval	108 nests
Leslie & Rose Nemeth at Yellow Creek	94+ nests ¹
Ian Lochtie at Kelliher	88 nests
Bob Gillard & Shirley Norlin at Wynyard	80 nests
Peter Boychuk at Crystal Springs	61 nests
Bob Robinson at Simpson	52 nests
Maurice Mareschal at Birch Hills	48 nests
Wayne Harris at Raymore	42 nests

¹Owls at another six nests banded by Wayne Harris in 1986

TREE CLIMBERS

Volunteers have always been needed to help with climbing trees. To climb 20 trees, many difficult, and band up to 61 nestlings in one day, would surpass the stamina of most men. We like to have three or even four climbers taking turns. This has become increasingly important as my knees and ankles become increasingly arthritic due to wear and tear as I grow older.

¹Paper presented at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

²Stuart Houston is Professor of Medical Imaging, University of Saskatchewan, Saskatoon, Sask.

Amazingly, volunteer climbers have always appeared when needed; some years I have had more offers than could be accommodated. Some biology students, at the high school or University level, come because of an interest in birds; although our rule is that we stop only for "lifers", it is a rare weekend when I cannot show them a species new to their life list. Some come with an interest in photography and others for sheer adventure. Some come to meet the nicest farmers in Saskatchewan -- and their daughters! Some have helped me from dawn to dark on every May weekend for several years in succession, while others don't come a second time!

My helpers have included city boys, farm boys and medical doctors. For several years I had physical education students, two of whom were ranked second in Canada for their weight class in wrestling; one of them, John Hanbridge, successfully wrestled with -- and banded -- an adult female Great Horned Owl when she delayed leaving her nest.

COSTS

Owl banding is an expensive proposition for the master bander. Food and transportation are provided for the volunteers, as well as hotel expenses when we overnight. My wife, Mary, fills a large cooler with beef, ham, turkey, and peanut butter-and-raisin sandwiches, cookies and gallons of iced tea. A four-wheel drive vehicle is a necessity. We have travelled as many as 2000 km on a 3-day long weekend, with major expenditures for gas, oil, tires and general wear-and-tear. Direct costs average about ten dollars per nestling owl banded.

In an average year, six female owls in one hundred will puncture the bander with their talons while he is up the nest tree. This necessitates a tetanus booster shot at a nearby hospital. Only once, near Strasbourg on 20 May 1979, did both adult owls attack the bander -- the female scoring eight direct hits and the male two, while John Hanbridge banded two nestlings. Since 1964 we have worn hard hats and safety goggles. Although I've had my goggles punctured and many gashes in my leather jacket (fig. 1), we've had no partial loss of eyesight as was experienced by Dick Lumsden near Edmonton, Alberta (Lumsden 1960). To date no climber has broken any bones.

BENEFITS

Perhaps the process has been more important than the project. My activities have increased public awareness of raptors in general and owls in particular. This has been most evident at Yellow Creek and Crystal Springs, where in the early 1960s the "only good owl was a dead owl", local farmers and their families are now interested in owls, and have developed some understanding of their niche in nature. One year I was the invited

speaker at Crystal Springs high school graduation ceremonies. No one can say how much influence I have had on my young climbers, since some of them had a career in biology in mind before they met me. I do believe that all have a strong conservation ethic and some after a period of decreased outdoor activity, are now instilling this ethic in their children. I follow their careers with interest and take a fatherly pride in their achievements.

I will mention only one nest finder and two climbers specifically. Rosemary Nemeth graduated from a two-year resources technology program and became Saskatchewan's first female conservation officer, before earning a University degree in biology, but her farmer father has continued to locate owl nests every year. Lorne Scott of Indian Head and Wayne Harris of Raymore, high school students when I first visited their owl nests, have gone on to obtain master banding permits of their own. Lorne, the naturalist for the Wascana Park Authority in Regina, has been president of both the Saskatchewan Natural History Society and the Saskatchewan Wildlife Federation and was the first recipient of Canada's annual Roland Michener Conservation Award. Wayne Harris is office manager of the Saskatchewan Natural History Society and with his wife operates an environmental consulting service.

This unplanned project, which grew irresistably, without funding or support of any kind, has added to scientific knowledge. Papers presented or cited at this conference indicate some of the things we have learned concerning longevity and the unexpected southeasterly movements of the Great Horned Owl, as well as its cyclical success, so closely tied to the 10-year cycle of the Snowshoe Hare.

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Capture Techniques for Owls¹

Evelyn L. Bull²

Information on capture techniques for owls--great gray (*Strix nebulosa*), spotted (*S. occidentalis*), boreal (*Aegolius funereus*), northern saw-whet (*A. acadicus*), and western screech (*Otus kennicotti*)--was presented by Gregory D. Hayward, Gary S. Miller, Robert W. Nero, and Evelyn L. Bull.

Hayward used bal-chatris, mist nets, and dip nets on the end of poles to capture three species of small owls. Bal-chatris were effective for capturing boreal and western screech owls, but not for northern saw-whet owls. The double-topped bal-chatri trap had 80 2.5-cm-diameter nooses made of 3-kg-test monofilament line (fig. 1). To trap unmarked boreal owls during the spring, Hayward placed 10 bal-chatri traps near a large mist nest. At dark, a recorded territorial song of the owl was played for 20 min each hour throughout the



Figure 1.--Boreal owl captured on a bal-chatri. Photo by Pat Hayward.

night; traps and mist nets were checked each hour. To recapture radio-tagged owls, a bal-chatri was placed under the roosting owl during the day.

A small mist net, 2.5 m long and 1.5 m tall, was effective for capturing radio-tagged boreal owls (fig. 2). The net was placed in front of the roosting owl in a shaded location, and a mouse was tethered behind the net. When the owl flew into the net, observers standing 1-2 m away immediately captured the bird. Poles supporting the net were light weight fiberglass rods.



Figure 2.--Boreal owl (arrow) in a mist net with a mouse tethered on the left side of the net between 2 upright sticks. Photo by Greg Hayward.

Hayward captured boreal, northern saw-whet, and western screech owls from their day roosts, with a dip net on a 5.5-m fiberglass extension pole. The oval hoop frame was 70 cm long and 45 cm wide; the net was made of mist net material. Hayward found that a slow steady approach to the owl was more effective than a fast one. If two people were available, one could distract the owl while the other worked the net up toward it.

¹Workshop presented at the Northern Forest Owl Symposium, Winnipeg, Manitoba, February 3-7, 1987.

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To capture spotted owls, Miller used a noose-pole, a 6-m long, telescoping fiberglass pole with a noose made of a flexible 2-mm-diameter plastic cord. The owls were located by calls. When a bird was sighted, a tethered deer mouse (*Peromyscus maniculatus*) was used to lure the owl close enough to put the noose over its head and tighten it around the neck. The owl was quickly lowered to the ground. Two split rings, tied 95 mm apart, kept the noose from choking the owl. Other techniques used to trap spotted owls included mist nets, bow nets, bal-chatri traps, and dip nets.

Nero had excellent success trapping great gray owls in Manitoba during the winter with a casting rod and fishing net (fig. 3). A simulated mouse lure on the end of the line was cast onto the snow within sight of the owl (figs. 4 and 5). The lure was reeled past a second person who netted the owl as it flew after the mouse. The technique worked well for hungry owls that had not been previously caught by this method.



Figure 3.--Fishing rod and net used to capture great gray owls. Photo by B. Ratcliff.

Nero also used a verbail to capture great gray owls. A live mouse in a cage was placed on the snow, and the verbail, mounted on top of a post, was set upright to act as a perch. When the owl landed on the post, its legs were caught in the noose.

I have used five techniques to capture adult great gray owls during the nesting season, including bal-chattris, mist nets, net-guns, noose poles, and a trap operating on the same principle as a verbail. Bal-chattris were most effective for birds that had never



Figure 4.--Robert Nero with mouse lure used to capture great gray owls. Photo by H. W. R. Copland.

been trapped before (fig. 6). Two gerbils (*Gerbillus* sp.) were used for bait, and nooses were made from 18-kg-test monofilament line.

Mist nets were used with various forms of bait including gerbils, juvenile birds, common ravens (*Corvus corax*), or great horned owls (*Bubo virginianus*) (fig. 7). In several cases, mist nets were suspended at least 15 m above the ground near the nest to capture the male owl when he delivered prey.

A noose-pole, similar to that described by Miller, was used to capture female great gray owls after the young had fledged and were handled. The females were very aggressive at this time and were easily noosed.

The net-gun was used to capture birds that could not be caught by any other method. It was only used to capture owls when they were perched low to the ground or were readily accessible from the ground. The net wrapped around the bird and the branch it was sitting on (fig. 7).

Many owls were caught on a trap designed to tighten a noose around the bird's legs when it landed on a tethered gerbil (fig. 8). The advantage of this method was that birds that



Figure 5.--Great gray owl descending on mouse lure. Photo by Robert R. Taylor.

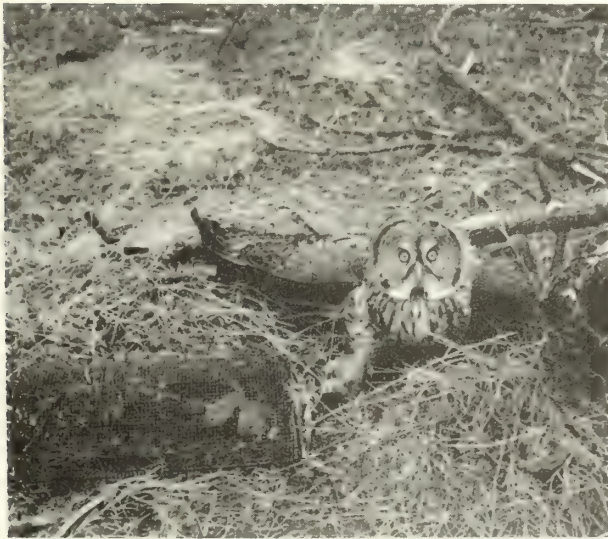


Figure 6. Great gray owl caught on a bal-chatri; gerbils were used as bait. Photo by Evelyn Bull.



Figure 7. Great gray owl caught in a net shot from a net-gun. Photo by Evelyn Bull.



Figure 8. Trap designed to catch the owl by a noose that tightens around its legs when it lands on prey. Photo by Evelyn Bull.

did not get caught in the noose took the gerbil anyway and did not become trap-shy.

In summary, many techniques have been designed to capture a variety of owls. Some species become trap-shy after a single experience, even if they are not captured. Different techniques are suited to different species because of differences in their behavior and habitat. Ease of trapping can vary by region because availability of prey differs; hungry birds are generally easier to trap than satiated ones.

Owl Telemetry Techniques¹

Thomas H. Nicholls² and Mark R. Fuller³

Abstract.--Successful radio-tracking techniques have been developed for many species of forest owls. These techniques have provided data about movements and behavior that could not be obtained in any other way. The objective of the telemetry workshop was to discuss various radio-tracking methods and to provide participants with telemetry references and a list of suppliers.

INTRODUCTION

Radio-tracking is a relatively new, revolutionary technique for studying the ecology of free-ranging animals. The history of wildlife radio-tracking spans about 25 years. The invention of small transistors and powerful batteries made it possible to build transmitters small enough to be carried by many species of animals (fig. 1). This technology allowed wildlife biologists and electronic experts to develop radio-tracking techniques to determine the precise location of individual animals. Portable radio receiving units enables a researcher to locate and then observe animals frequently (fig. 2).

The most common applications of radio-telemetry are to obtain information on the natural movements and behavior patterns of individual animals. Specifically, applications include the estimation of home range, habitat use, predator-prey relationships, survival, activity periods, effects of weather and other factors on activity, daily and seasonal movement patterns, dispersal and migration patterns, and social relationships, such as territoriality (Nicholls and Fuller; this symposium). Telemetry also can be used to locate nests and roosts either from the ground or air (Nicholls et al. 1981). In addition, bio-telemetry can be used for measuring physiological processes of free-ranging animals (Kuechle et al. in press) (fig. 3).

¹Telemetry techniques workshop presented at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service, General Technical Report RM-142.

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EARLY DEVELOPMENT OF OWL RADIO-TRACKING TECHNIQUES

Workshop participants viewed a film depicting the development of owl tracking with a semi-automatic system for monitoring animal movements on the University of Minnesota's Cedar Creek Natural History Area (CCNHA) 30 miles north of Minneapolis, Minnesota USA (Cochran et al. 1965). The system was primarily designed and put together by William Cochran, who many agree has contributed more to the field of wildlife telemetry than any other single person. The system utilized two towers 1/2 mile apart (70 ft and 100 ft high) each with directional receiving antennas (fig. 4). The antennas rotated every 45 seconds and, under ideal conditions obtained 1,920 locations per animal every 24 hrs for up to 52 animals simultaneously. Received signals were displayed by indicator lights, then photographically recorded. The film was read at selected intervals to obtain degree bearings from

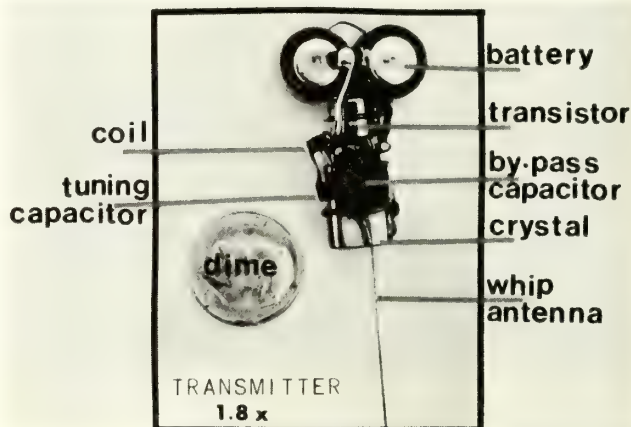


Figure 1.--Components of a 5 gram radio transmitter.



Figure 2.--Portable receiving units can be used with different antenna systems, such as the loop antenna (top) and Yagi antenna (bottom), to locate and observe owls under field conditions.

each tower. These data, time, and date were entered in a computer and programs calculated animal locations and plotted them on a map of the CCNHA (fig. 5). The resulting information was used for ecological studies of many species including owls (Nicholls and Warner 1972) (fig. 6). Techniques and equipment developed at the CCNHA are now in world-wide use for research on many species of animals.

Radio-tracking techniques for owls were developed for three species of owls using the CCNHA radio-tracking system: the great horned owl (*Bubo virginianus*), the barred owl (*Strix varia*) (Nicholls and Warner 1968) (figs. 7 and 8), and the northern saw-whet owl (*Aegolius acadicus*) (Forbes and Warner 1974) (fig. 9). These studies paved the way for other raptor telemetry because the technique was shown to have little influence on the natural behavior of radio-tagged birds. Since the 1960's, radio transmitters and attachment techniques have been improved and

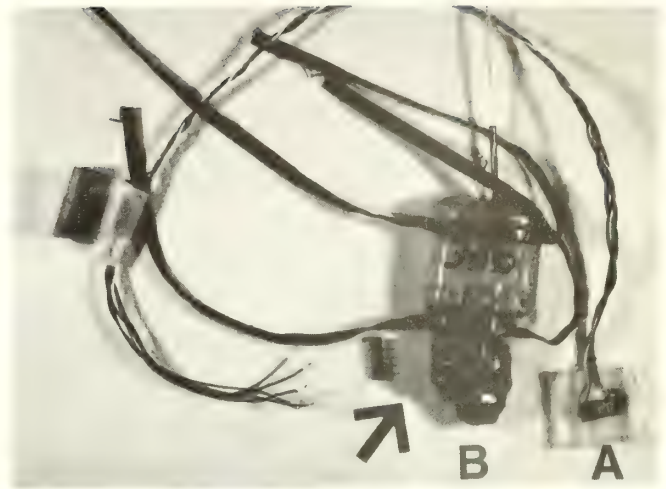


Figure 3.--A radio transmitter used to study gastric motility in barred owls. The gastric sensor (A) is surgically implanted and plugged into (arrow) a back-pack transmitter (B) that transmits an owl's location and gastric activity.

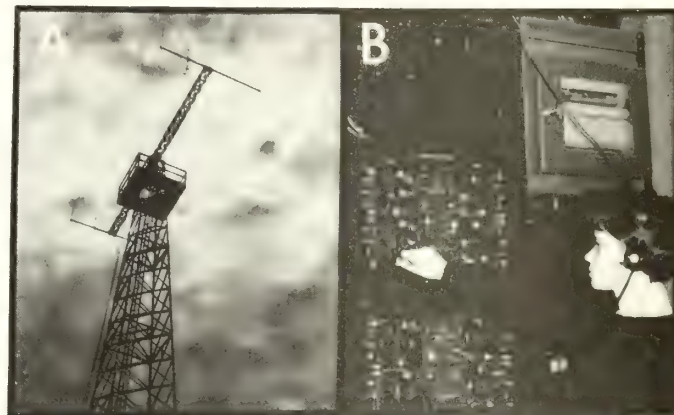


Figure 4.--(A) A 100 foot radio-tracking tower located on the CCNHA. (B) Each owl was assigned a different radio frequency and a receiver was tuned in to each of two radio-tracking towers. All owls with transmitters could be monitored simultaneously.

refined (Dunstan 1972, Amlaner and Macdonald 1980, Cochran 1980, Kenward 1985). For example, Evelyn Bull (personal communication) put radio transmitters on 58 great gray owls (*S. nebulosa*) from 1983 to 1986. Transmitters weighing about 22 grams transmitted for at least 1 year at which time they were replaced. The transmitter with whip antenna was put on the back of a bird with a tubular teflon ribbon back-pack harness in a figure eight type of configuration. Some birds carried them 3 years, and none showed any abrasions or apparent ill effects from the transmitters. Transmitters built today are more reliable, smaller, lighter, more durable and are economical, considering the amount of information that can be gained and that some data cannot be obtained in any other way.

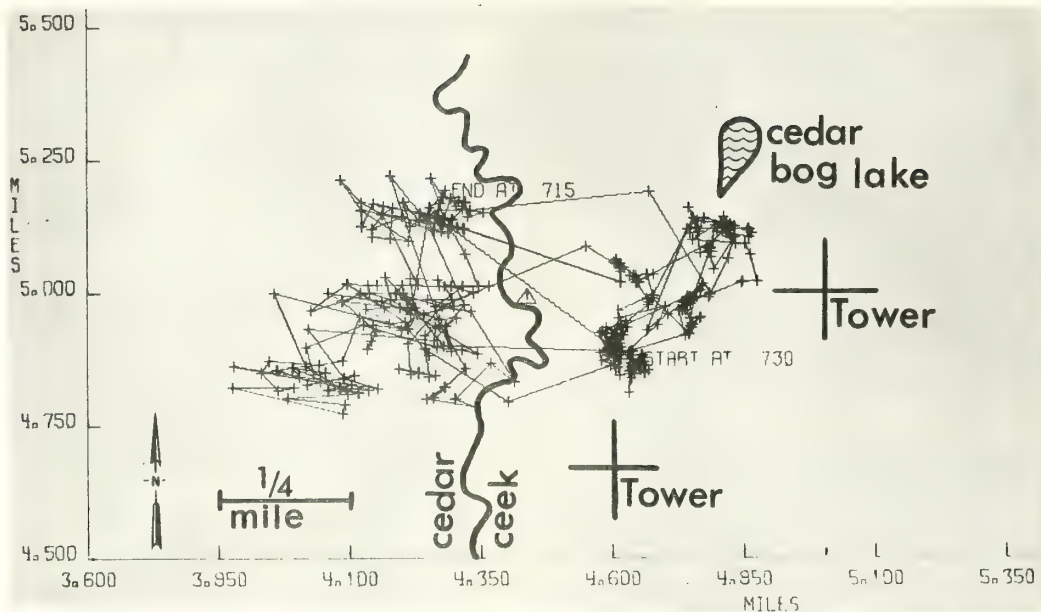


Figure 5.--A computer-generated plotter map of barred owl movements. Each plus mark denotes one or more owl locations. Lines between plus marks are movements between locations. Note how the deciduous woodlots in fig. 6 are outlined by owl movements as seen in fig. 5.

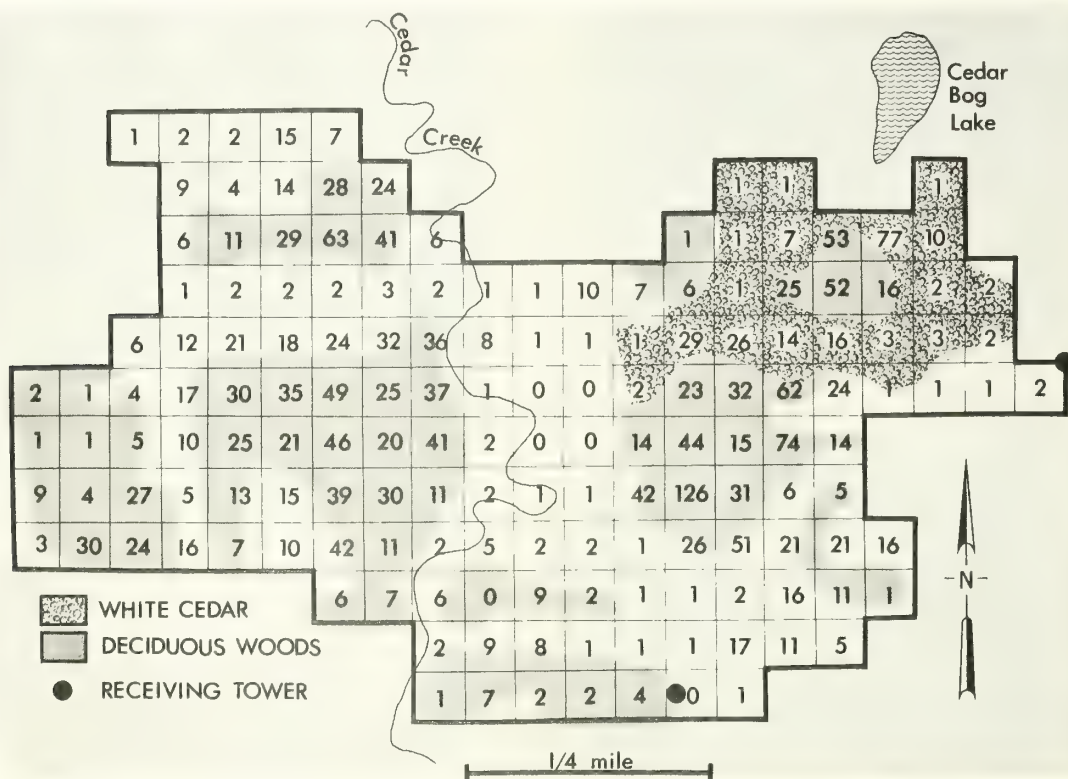


Figure 6.--The 258-acre home range of a barred owl from July 15 to September 30. Each square represents 1.6 acres; the numbers in squares indicate the total number of locations within each square as determined by degree bearings obtained from two radio-tracking towers on the CCNHA. The size of the home range was determined by drawing a line around the outer most squares containing locations and multiplying the number of squares inside by 1.6. Habitat use was determined by assigning a vegetation type to each square. Note how little use was made of fields or marshes (white areas) compared to intensive use of deciduous woods (shaded areas).

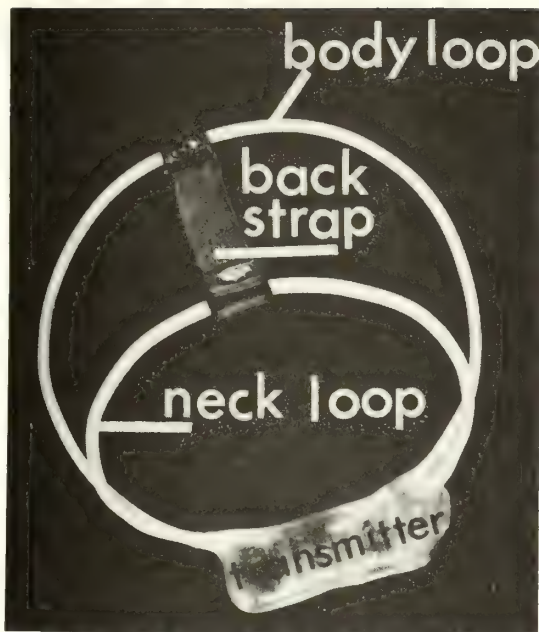


Figure 7.--The first radio transmitter harnesses placed on great horned and barred owls in the early 1960's weighed 70 to 90 grams and transmitted up to 200 days with signals detected for up to 3 miles by the CCNHA radio-tracking towers. Since then, refinements and new technology allow transmitters to be much smaller, lighter, and more reliable.

OWL TELEMETRY CONSIDERATIONS

Radio telemetry is an excellent tool for studying nocturnal birds such as owls. Many results reported in this symposium were obtained using radio-tracking to obtain data. The following summarizes some of the important considerations when using telemetry to study owls.

Transmitter attachment techniques are as diverse as the size, shape, weight, and application of the transmitters. Before trying new methods and equipment, it is advisable to check with researchers experienced with similar techniques and species. When using telemetry for the first time or developing new methods, work with captive birds in suitable flight cages to identify negative effects that transmitter attachments might have. Observations of takeoff, flight, landing, attacking, capturing, killing, and eating prey, etc. should be made to make sure that transmitters do not interfere with behavior (fig. 10). Kay McKeever, Owl Rehabilitation Research Foundation, RR #1, Vineland Station, Ontario LOR 2E0, offered use of her facilities to test radio transmitters on owls.

Before beginning a radio-tracking study, determine for how long and how far signals must be received from the owls. Large, heavy batteries provide more power for longer life or stronger radio signals. Consider compromising between

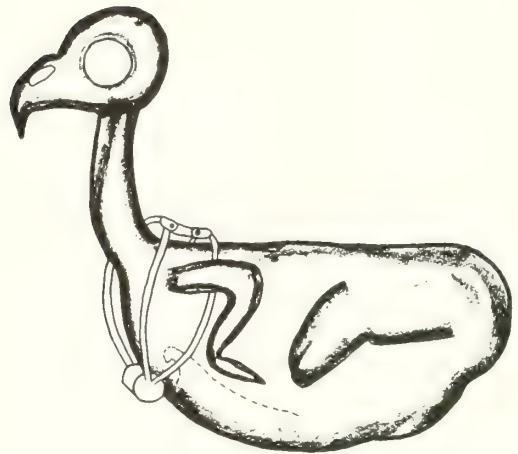


Figure 8.--Position of the first transmitter harness (fig. 7) developed in the early 1960's as it appeared on the body of an owl without feathers.

signal strength, life, and weight. Make sure the company supplying the equipment understands your needs and has experience with similar applications. Remember that design engineers usually provide optimistic estimates of transmitter life that might not be met under variable field conditions, especially low temperatures. The duration of the study can also determine attachment techniques. Many harness materials last for months or years and can only be removed after recapturing the owl. Recapture is often difficult, expensive, and time consuming. Presently, there are no reliable methods for detachment at pre-determined durations; however, some "drop off" harness attachments have been developed (Boshoff et al. 1984, Karl and Clout 1987).

Tail mounts must be used with light-weight transmitters, and are lost when the feathers are moulted (Fitzner and Fitzner 1977, Kenward 1985) (fig. 11). We suggest that the transmitter supported by a single rectrix be no more than 2% of the owl's body weight because tail-mounted transmitters may stimulate the tail feathers to moult prematurely. Back-pack transmitters require suitable harness material; teflon ribbon and coated, flexible wire have been useful on owls (Dunstan 1972, Smith and Gilbert 1981). Glued-on transmitters (Raim 1978) have not been used often on owls. Solar-powered transmitters are lightweight and can be used alone or with rechargeable batteries to provide nighttime coverage. Solar transmitters must be attached so the birds cannot preen the transmitter under the feathers. Dense vegetation will inhibit or reduce the effectiveness of solar-powered transmitters.

Recent articles by Caccamise and Hedin (1985) and Pennycuik and Fuller (in press) deal with bird size and the potential effects of transmitter weight. In general, transmitter weight should be a smaller percentage of the body weight for large birds than for small birds. Transmitter weight can affect potential maximum velocity, maximum power, endurance, and maneuverability of birds. After a transmitter is attached, an owl might reduce its activity for a few days as it adjusts to the harness and transmitter (Nicholls 1973).

In the United States, biologists need a frequency authorization or license from the Federal Communications Commission to conduct telemetry studies. There are severe restrictions on frequency, power output, numbers of transmitters per unit area, etc. (Kolz 1983). The U.S. Fish and Wildlife Service Bird Banding Laboratory, Laurel, MD 20708 USA, provides brief information about the regulations. In addition, there are regulations that must be followed while using aircraft to radio-track animals. Safety is of prime consideration. Placement of antennas on aircraft must conform to certain standards and should be checked by an expert. One workshop participant told of a potentially serious situation in which an aircraft flew into clouds where icing developed, breaking off an antenna element that could have caused an accident. Use an experienced pilot who concentrates on flying while the biologist concentrates on animal



Figure 9.--A back-pack radio transmitter with a whip antenna was originally developed for use on northern saw-whet owls and subsequently used on many other species.



Figure 10.--Captive great horned owls wearing radio transmitters were studied in flight cages 3 months to make sure that transmitters did not affect the birds' natural activities. Similar studies should be done on owl species for which telemetry techniques have not been perfected.

tracking. Pilot error has caused most accidents related to aerial radio-tracking. Aerial tracking in mountainous areas can be extremely dangerous. Listening to radio signals for extended periods over the background noise of a plane can cause hearing loss. Biologists should use visual indicators on radio receivers as much as possible during prolonged aerial tracking. Gilmer et al. (1981) and Mech (1983) provide excellent advice for those who need to use aerial radio-tracking.

Braun Hill and Clayton (1985) review nocturnal observation techniques. A potentially useful technique for use on owls is the betalight. Betalights are self-contained, sealed

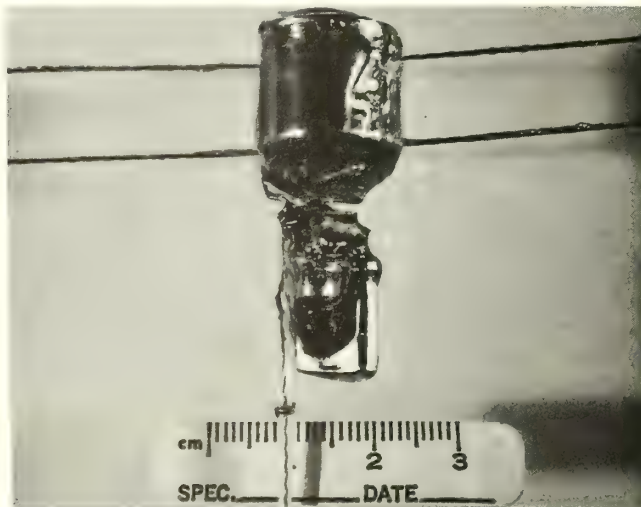


Figure 11.--A light-weight radio transmitter used for owl tail mounts.

glass capsules filled with tritium gas and internally coated with phosphor. The tritium, which is radioactive, emits low-energy beta particles that strike the phosphor coating, causing it to emit a continuous, visible glow. Gregory Hayward (personal communication) tested betalights in conjunction with radio telemetry to make observations of foraging boreal owls (*A. funereus*). Owls fitted with betalights attached to backpack-mounted radio transmitters were only slightly easier to observe than radio-marked owls without betalights observed with night vision goggles. However, a betalight attached to a radio antenna (fig. 12) so it is held free from an owl's plumage may have great potential, but more testing is needed.



Figure 12.--A betalight (arrow) attached to a radio antenna on a transmitter carried by a boreal owl.

Unless you are electronically inclined, don't try to build your own equipment. When all of the advantages and disadvantages of buying or making radio transmitters and receiving equipment are considered, most participants concluded that it is better to buy equipment from experienced companies than it is to make it themselves.

CONCLUSION

Radio telemetry has contributed to major advances in the study of owl behavior and ecology. Biotelemetry will make more significant contributions as new technology is developed and applied. Spatial requirements and habitat use by various owl species are two important factors that must be determined for effective conservation and management of viable populations of northern forest owls. Radio telemetry helps provide this information.

ACKNOWLEDGMENTS

The authors would like to thank the workshop participants for sharing their owl radio-tracking experiences. We would also like to thank G.D. Hayward for fig. 12 and M. Nelson for reviewing the manuscript.

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SUPPLIERS OF TELEMTRY MATERIALS

The use of firm or corporation names in the following list is solely for the information of the reader. This list is by no means exhaustive and does not constitute an official recommendation or endorsement of any products or services to the exclusion of those offered by other companies.

Advanced Telemetry Systems, Inc.
470 First Avenue North
Box 398
Isanti, Minnesota 55040
612-444-9267

Austec Electronics Ltd.
#1006, 11025-82 Ave.
Edmonton, Alberta, Canada T6G 0T1
403-432-1878

AVM Instrument Co., Ltd.
2368 Research Drive
Livermore, California 94550
415-449-2286

Bally Ribbon Mills
23 N. 7th St.
Bally, Pennsylvania 19503
215-845-2211
(For teflon ribbon harness material)

Beacon Products Co.
360 East 4500 South
Salt Lake City, Utah 84107
801-265-9687

Biotrack
Stoborough Croft
Grange Road, Stoborough
Wareham, Dorset BH20 5AJ
England

B&R Ingenieurgesellschaft mbH
Johann-Schill-Str. 22
7806 March-Buchheim, West Germany

Custom Electronics of Urbana, Inc.
2009 Silver CT. West
Urbana, Illinois 61801
217-344-3460

Custom Telemetry & Consulting
185 Longview Drive
Athens, Georgia 30605
404-548-1024

Holohil Systems Ltd.
RR #2
Woodlawn, Ontario, Canada KOA 3M0
613-832-3649

L.L. Electronics
P.O. Box 247
Mahomet, Illinois 61853
215-586-2132

Lotek Engineering Inc.
11 Young St. S.
Aurora, Ontario, Canada L4G 1L8
416-727-0181

Microwave Telemetry
610 Chestnut Ave.
Towson, Maryland 21204

Midwest Telemetry
Judy Montgomery
P.O. Box 773
Urbana, Illinois 61801
217-367-1904

Narco Scientific
(Short Range Bio-Medical)
7651 Airport Blvd.
P.O. Box 12511
Houston, Texas 77017
713-644-7521

Remote Monitoring Systems
P.O. Box 2155
Walla Walla, Washington 99362
509-529-1060

Scien-O-Tech Consultants Ltd.
Box 14426 Box 87054
Nairobi Mombasa Kenya

J. Stuart Enterprises
P.O. Box 310
Grass Valley, California 95945
916-273-9188

Telemetry Systems, Inc.
11065 N. Lake View Dr.
P.O. Box 187
Mequon, Wisconsin 53092
Owner - Owen Royce
414-241-8335

Telonics
932 Impala Ave.
Mesa, Arizona 85204-6699
Owner - Dave W. Beaty
602-892-4444

Wildlife Materials Inc.
R.R. 1
Carbondale, Illinois 62901
Wildlife Consultant - R.E. Hawkins
618-549-6330

Owl Management Techniques¹

Katherine V. Haws²

Wildlife management issues and programs involving northern owls were the subject of this workshop. Programs currently underway in various parts of the United States and Europe were summarized by the panelists.

Management for northern owls in the Pacific Northwest has centered around endangered species concerns, primarily the spotted owl. The U.S. Forest Service and conservationists have been embroiled in a decade long controversy involving the spotted owl as an indicator species of old growth fir spruce and hemlock forests. These forests have almost all been cut, and yet studies by ornithologists on the Spotted Owl Recovery Committee have recommended that old growth forest tracts of 1400-4500 acres in size be set aside for each pair of owls. A recommended owl population size for the region is 1500 pairs.

Management plans and actions for several forests in this region have not complied with these requests for habitat protection, and the result has been an embittered conflict between many factions.

Elsewhere in the northwest, the boreal owl has received priority as a candidate species for research. The effects of alternative logging practices, sale sizes and sale distribution on boreal owl populations is being studied in Idaho. Nest boxes are being erected for this species and other cavity nesting species on Idaho's National Forests.

The flammulated owl has been the focus of research and management for northern owls in the Rocky Mountain States. Census/survey efforts, and nest box placement have also been initiated on several National Forests in this region.

In Manitoba, an agreement between a paper/wood corporation and the Manitoba Department of Natural Resources, has been signed which sets aside a 12 mi.² area for owl habitat preservation. Great gray owl research receives high priority within the Manitoba Nongame Program, and has received wide backing from many sources, including World Wildlife Fund.

Management programs for the great gray owl in Manitoba have included placement of artificial nest structures and creating habitat reserves.

In the midwest states several northern owls have been placed on state endangered species lists, including the short-eared owl.

Management projects have included basic census and survey projects, as well as placement of nest structures for barred owls and great gray owls. These two species have been selected as indicator species by the U.S. Forest Service-Chippewa National Forest, and management is yet in the planning stages.

Between 5-15% of the timber resources on the Chippewa National Forest have been set aside on an old growth rotation, resulting in habitat protection for northern owls inhabiting these community types.

In Minnesota, the Nongame Wildlife Program of the Department of Natural Resources has initiated several management projects. A publication entitled "Woodworking for Wildlife" describes how to build many nest boxes, including nest boxes for barred owls, great gray owls, and great horned owls. This publication has been made available to the public and as a result, many nest structures have been put up.

1 Summary of workshop comments at the symposium, Biology and Conservation of Northern Forest Owls, Feb. 3-7, 1987, Winnipeg, Manitoba. USDA Forest Service General Technical Report RM-142.

2 Nongame Specialist, Minnesota Department of Natural Resources, Bemidji, MN. Other workshop panel members were: Thomas Hamer, Ronald Ryder, Harriet Allen, and Geir Sonerud.

Forest management guidelines which consider the needs of wildlife have been completed, and these guidelines address issues such as protection of riparian areas, and snag trees.

A management plan for the Roseau Bog Owl Management Unit in Roseau County, Minnesota has been completed. This management plan addresses needs of, among other wildlife species, the great gray owl on the 14 mi.² unit, and makes recommendations to harvest timber without adversely affecting owl populations in the area.

Currently, most state and federal agencies are at the point of obtaining basic habitat, range and population data for our northern owl species. Until these base-

line data are obtained, management programs cannot be effectively initiated. At this time it is difficult to predict specific impacts of forest management activities such as clear cutting, chemical release, and other silvicultural practices on particular species.

In future years, research will most likely become more applied in scope, in order to answer some of these questions.

Currently, management programs involve habitat preservation, placement of nest structures, protection of nest trees, education efforts, old growth forest protection and initiation of an ecosystem approach to habitat management.

Owl Census Techniques¹

Dwight G. Smith²

General Census Considerations

Dwight G. Smith and Tom Carpenter³

Owls are notoriously difficult to count; most species are wholly nocturnal, and roost in concealed locations during daylight. Consequently, methods for estimating the size of owl populations are not well developed. Indeed, of several recent reviews of methods for estimating animal populations, only Ralph and Scott (1981) include chapters on censusing nocturnal birds.

Techniques used to detect and count owls differ considerably in methods of collection, analysis, and presentation of data. There is an urgent need to determine and standardize the method or combination of methods which provides the most accurate counts for each species.

Methods for detecting and counting raptors are summarized by Fuller and Mosher (1981). Owl census techniques include visual searches on foot, tallying numbers of owls singing spontaneously, locating roosts and nests by passerine behavior, and using tape recorded song to elicit responses.

Prior to the advent of readily available portable tape recorders and telemetry equipment, most censuses of owls were conducted by foot or vehicle searches (Craighead and Craighead 1956; Orions and Kuhlman 1957, Hagar 1957, Smith and Murphy 1973). These searches involved intensively looking for owl roost or nest sites, flushing the owl or finding evidence of owl presence such as kills, owl feathers or pellets. The success depended greatly on conspicuousness of the owls and observer acumen. Searches work best with larger species in woodland habitat or snowy owls (*Nyctea scandiaca*) in open habitat. For woodland species, at least, foot searches are generally marginally accurate and time consuming.

Another owl census technique involves the use of listening stations at which observers count spontaneously singing owls. This technique is equivalent to the call counts used by wildlife biologist to census a variety of game birds. Baumgartner (1939) estimated nesting territories

of great horned owls in riparian woodlands along the Missouri River by noting presence of singing pairs, while Miller (1930) augmented spontaneous song with vocal imitations to investigate the territoriality in great horned owls. In Sweden, Holmgren (1979) counted singing Tengmalm's owls (*Aegolius funereus*) along a point transect. Counts of singing owls depend on seasonal song activity, which may vary considerably in timing and frequency for different owl species. Additionally, males lacking territories and females of some owl species may not spontaneously sing, so censusing results will be distorted.

McPherson and Brown (1981) used playback of tape recorded song during daylight hours to locate roost or nest sites of screech owls that responded and also to elicit mobbing behavior of passerines, which oriented to the owl's location. They were able to consistently obtain screech owl locations in their North Carolina piedmont study area.

Eastern Screech Owl responding vocally and visually to playback of tape-recorded song.

Photo by A. Devine



¹Workshop held at the symposium, Biology and Conservation of Northern Forest Owls, Winnipeg, Manitoba, Canada, February 3-7, 1987.

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Recently, playback of tape recorded song has been used to census a variety of avian populations (see Ralph and Scott, 1981). Johnson et al., (1981) noted usefulness of this technique especially for secretive, nocturnal birds, including owls, that cannot otherwise be reliably censused. This technique is based on the territorial behavior of owls; song playback or vocal imitations within their territory will produce a vocal or visual response by the owl attempting to defend its territory against the "intruder." Song playback has been used to survey a number of owl species and has proven most useful in extensively wooded habitat and rugged terrain.

Field Techniques

Methods chosen to count owls should vary with the activity patterns and behaviors of the owl species being censused. Spacing of listening stations, song playback stations, or amount of area searched on foot should be determined by the distance a species will respond to playback, distance the song can be heard, and the territorial size; an individual owl may be counted at two or more stations spaced too close, while some territories might be missed if stations are too far apart. If time and equipment permit, average territory size may be determined using radio-marked owls.

The role of vocalization and associated behaviors in establishing and defending an owl's territory must be considered when using song playback. Most species of owls have a varied repertoire of songs and other vocalizations; some may be more effective in eliciting responses. For example, eastern screech owls show distinct seasonality of warble and whinny song (Smith et al. this proceedings) while Johnson et al., (1981) found that vocalizations of a caged female were effective in obtaining responses by western screech owls (*Otus kennicottii*) in southern Arizona.

Songs of most North American owls are available on record or tape cassette (e.g., Field Guide to Bird Songs and Field Guide to Western Bird Songs) which are available from Cornell Laboratory of Ornithology. Jon Winters (pers. commun.) is currently preparing a record set of the vocalizations of all North American owls. For maximum effectiveness, we recommend that songs be obtained by directly recording singing owls. This will ensure correct intervals between song and silent periods, and also incorporate any local song dialects.

Speakers should be omnidirectional and placed away from the observers/listeners to increase chances of hearing the sometimes brief responses. Some observers prefer to walk in a circle 30 or more meters around the speaker but we do not recommend this procedure for all owls; individuals that approach before responding may be frightened, similarly, individuals that approach but do not respond also may not be detected.

At least four types of responses by owls have been noted: (1) the owl sings from a distance but

does not approach the song playback station, (2) the owl initially sings from a distance then approaches the song playback station and sings again, (3) the owl silently approaches the playback station, and begins to sing and (4) the owl silently approaches the song playback station but does not vocalize.

Factors Affecting Responses

Vocalization and other responses to song playback may vary with time, weather conditions, moon phase, and background noise. How these factors singly or in combination influence the response of owl species must be determined to effectively evaluate census results.

Four temporal factors which may influence response frequency and type of response for species of owls include time of night, hours after sunset or hours before sunset, and season. Many species have distinct peaks of activity for 2-3 hours after darkness and before sunrise, and are less active during the remainder of the night. Species that show a pronounced seasonal rhythm in responsiveness to playback include eastern screech owls (Carpenter 1985, Smith et al., this proceedings), whiskered owls (Martin 1974), barred owls (Smith 1978), and spotted owls (*Strix occidentalis*) (Forsman et al., 1984). Several of these species are most responsive during fall and winter, corresponding with territorial establishment and defense, but become more secretive and less responsive during the spring breeding season.

The single most important weather variable negatively influencing response to song playback is wind (Siminski 1976, Forsman 1983, Smith et al. this proceedings). The decreased response rate may be due to limited range of song playback under high wind conditions, the inability of observers to hear or see responding owls, or the fact that owls may be comparatively inactive because of difficulties involved in efficient flight or foraging; perhaps they are unable to hear prey as well. Temperature extremes, especially low temperatures, decrease response rate of eastern screech owls (Beatty 1977, Casner 1974, Smith and McKay 1984, Carpenter, this proceedings).

Cloud cover and type of precipitation also may influence response rate of some owls, but as yet have not been sufficiently studied. Wolfgang Scherzinger (pers. commun.) has suggested that, for some European owls, changes in barometric pressure will stimulate increased activity, including spontaneous singing.

Johnson et al., (1979, 1981) found that response rates of western screech owls and elf owls (*Micrathene whitneyi*) varied with the lunar cycle, with both species being most active on clear, moonlit nights, but Smith et al. (this proceedings) was unable to document a similar relationship in eastern screech owls. Intensity and type of noise influenced screech owl response (Smith et al. this proceedings) although individuals varied considerably in tolerance to noises associated with human activity. Species



Eastern Screech Owl sunning at cavity entrance. Visual censusing necessitates that owls exhibit diurnal behavioral patterns that render them observable if not conspicuous.

Photo by A. Devine

such as the screech owl may be much more tolerant of human noises than other owl species.

Several biological and behavioral factors may influence response to song playback or general detectability; sex, age, breeding status, and number of breeding pairs in an area have been especially noted. Spotted owl response is lower during years when few pairs breed (Forsman 1983). Hirons (1976) reported that tawny owls sing more often when territories are small and adjacent. Wolfgang Scherzinger (pers. commun.) noted that in some European species, the older, established owls are much less responsive than younger owls.

Siminski (1976) and Springer (1978) found that female great horned owls are less responsive than males and thus more difficult to census. Conversely female eastern screech owls, especially those with territories, responded alone or dueted with their mates in response to song playback within their territory (Smith et al. this proceedings).

The presence of larger owls may also decrease responses. Bondrup-Nielsen (1984) observed that a boreal owl stopped singing when a great horned owl vocalized nearby. Marshall (1939) observed that a flammulated owl (*Otus flammeolus*) became silent when a spotted owl called.

An important factor that decreased the response frequency in eastern screech owls was accommodation of individuals to frequent or extensive song playback (Smith et al. this proceedings). Accommodation has also been found in tawny owls (Hirons 1976) and boreal owls (Bondrup-Nielsen 1984) and may in fact, occur in may owl species.

Negative Effects of Playback

Although song playback is effective in locating and studying owls, it should not be used

indiscriminately. Responding birds may vocalize for some time after playback, and could be more easily located by predators. Small owls are sometimes captured by larger owls, and some larger owls (spotted, barred, and great gray) have been recorded in the diet of great horned owls (Forsman et al. 1984, Bent 1938; Duncan, this proceeding, others).

Responding to playback reduces time for normal activities of the owl. In montane forests of Colorado, Palmer and Rawinski (1986) used song playback to locate boreal owls during September and October in order to avoid disrupting courtship. In addition, it may be possible for frequent and persistent playback to frighten owls from their territory or alter their territorial boundaries; although not documented in any North American species, this has been noted as a problem in Europe (Wolfgang Scherzinger, person. commun.). It is also possible that louder-than-normal playback continued for long duration may act as a super-stimulus, drawing owls from much longer distances than would otherwise occur.

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Census of Barred Owls and Spotted Owls⁴ Tom Bosakowski⁵

Both the barred owl (*Strix varia*) and spotted owl (*Strix occidentalis*) are birds of forested terrain. Their habitats are typically mature and old-growth forest that are often dominated by conifers. Given these conditions, the only practical method to estimate the abundance of these owls is the use of some playback techniques which induce the owls to reveal their presence.

Gould (1977) and Forsman et al. (1977, 1984) surveyed populations of spotted owls in California and Oregon, respectively, using vocal imitations or tape recorded broadcasts. Sutton and Sutton (1985) and Bosakowski et al., (this proceedings) also used both methods to survey barred owls in southern and northern New Jersey, respectively. Although some investigators of the barred owl have relied completely on the use of tape playback (Gutmore 1977, Smith 1978, Elody 1983, McGarigal and Fraser 1984, 1985, Kane and Valent 1986), all

have used different equipment, recordings, and sound wattage.

In northern New Jersey, Bosakowski et al. (this proceedings) found a high response rate (82.4%) of barred owls to vocal imitation or song playback during the breeding season. This rate was determined by 34 rechecks of known barred owl locations from which a positive response was recorded. This is a minimal response rate since we were unable to account for factors such as mortality or permanent relocation. Conversely, response rate during the non-breeding season was significantly lower (33.3%) suggesting that barred owls may be censused with reasonable accuracy during the breeding season, but surveys during the non-breeding season (Christmas bird counts) should be viewed with caution.

Elody (1983) believed that territory size of barred owls increased during winter and that males often vacated territories for most of the winter. Bosakowski et al., (this proceedings) found that both response rate and the number of responses by pairs decreased during winter, which hints at territory expansion and temporary pair-bond dissolution. Forsman et al., (1984) also found territory expansion in winter and similarly noted that response to calling was highest between March and September.

While most barred owl censusing has been conducted at night, both Elody (1983) and Bosakowski et al. (this proceedings) have found no apparent difference in barred owl response rate between

⁴ Presented at the Owl Census Techniques Workshop at the Symposium, Biology and Conservation of Northern Forest Owls, Winnipeg, Manitoba, Canada, February 3-7, 1987.

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nocturnal and diurnal censusing. These results are not entirely unexpected since Fuller (1979) noted that radio-marked barred owls exhibited considerable diurnal activity during the breeding season. Day censusing makes it possible to search remote, rugged terrain lacking roads or suitable trails. Although the spotted owl will also respond to imitation of its calls during the day (Gould 1974, Forsman et al. 1984), most censuses have been conducted at night.

During day censuses of barred owls, investigators should remain concealed while calling because this species is generally secretive and will often flush or remain silent if the observers are detected (Bosakowski et al., this proceedings). In contrast, the spotted owl is very tame and concealment is not necessary (Forsman et al. 1984).

Stearns (1947) and Smith (1978) believed that barred owl singing was audible up to 0.7-0.8 km, therefore, census stations can potentially be spaced 1.6 km to attain systematic coverage of an area. Responses less than 2 km apart may need to be checked to determine if the owls belong to the same or adjacent territories. This determination can be facilitated by (1) simultaneous or near simultaneous singing of adjacent pairs (2) by obvious natural boundaries (Smith 1978), (3) by boundaries such as developments and highways (Bosakowski et al., this proceedings), or (4) by confirming simultaneous occupancy of the adjacent territories. Since spotted owl ranges are considerably larger (Forsman et al., 1984) than barred owl ranges (Nicholls and Warner 1972, Fuller 1979, Elody 1983) caution should be exercised when analyzing the results of censuses with song playback. Both barred and spotted owls may maintain traditional territories for successive years (Bent 1938, Forsman et al. 1984, Bosakowski et al., this proceedings), even when the individuals have changed (Forsman et al., 1984, Nicholls and Fuller, this proceedings), thereby facilitating surveys conducted over several years.

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Census of Flammulated Owls⁶ Richard T. Reynolds⁷

Flammulated owls (*Otus flammeolus*) best respond to taped or vocal imitations (Marshall 1939, Winter 1971) of their primary song from the latter part of May through early July. However, after the eggs hatch (early July), paired males cease to quickly respond to song imitations (= broadcast) but non-paired males continue to respond through the summer (Reynolds and Linkhart 1987a). During May to early July, it is best to count singing males between 1 hr after sunset and about 1 hr before sunup. If a count of singing males must continue after egg hatch, the count should not begin before 2 hrs after sunset and should end 2 hrs before sunup. Nesting males forage intensively for their families and have little time for territorial defense during these periods.

During the responsive period (May to early July) males generally begin singing within several minutes of a broadcast, but a listening period of

⁶Presented at the Owl Census Techniques Workshop at the Symposium, Biology and Conservation of Northern Forest Owls, Winnipeg, Manitoba, Canada, February 3-7, 1987.

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at least 10 min. should follow each broadcast. A single broadcast bout should not exceed 1 min. It is not uncommon to have more than one male flammulated owl respond to a broadcast, and responding owls may continue singing after initial response. Neighboring males may be stimulated to sing, and as a result, the song response may spread over a wide area. Therefore it is advised to listen for several minutes before broadcasting at each new broadcast station.

Responding males may 1) begin singing without approaching, 2) approach while singing, or 3) come to their territory boundary before singing. On several occasions territorial males approached beyond their boundaries; some of these continued to sing as they did so, others approached silently and were noted perched quietly within 10 m of the broadcast station.

Because flammulated owls have quiet, low pitched voices, counters should be trained and tested for hearing capabilities before initiating a formal count. On clear, quiet nights, males singing from a ridge can be heard to 1.0 km. Due to the voice characteristics of the owl, however, it is difficult to estimate the distance to singing males. Rain, snow, wind, creeks, autos, and airplanes hindered counts of singing males. We recommend counting only on completely still nights. Moon phase has no apparent effect on the response of the males.

Linkhart et al. (in review) found that territorial boundaries of males frequently occurred along ridge tops. Therefore, counting routes are most efficient (number of responding males/distance traveled) when located along ridges. Ridge-top routes not only make for easier travel and increase the broadcast and hearing range, but expose the counter to more territories.

Because territories are approximately 400 m across (Reynolds and Linkhart 1987b), counting stations should be about 600-800 m apart in uniform terrain. In broken terrain, the distance between stations should be less; however, they should be no closer than 400 m. Counters must be aware that singing males may approach beyond their territories, especially if there are no intervening territories between the broadcast station and the approaching owl.

Not all singing males are necessarily nesting. In our studies, several responding males were unpaired for reasons probably related to

their age and/or quality of their territory (Reynolds and Linkhart 1987b). We have followed most of our counts of singing males with intensive nest searches (Reynolds and Linkhart 1984).

To estimate the density of flammulated owls on one of our study tracts, we used a modified territorial mapping technique during two nesting seasons (1980-1981). The procedure involved repeated entries by 2-3 widely-spaced persons onto the tract from different directions. After one of us broadcasted the primary song, responding males were quickly located and all subsequent song-trees used in a song bout were marked and mapped. When two or more males responded to broadcast, or when males were heard singing before broadcast, the census personnel divided and mapped the song-trees of each owl simultaneously. In both years we tallied 25-30 clusters of song-trees (territories), most of which were used in both years. In 1982 and 1983 we repeated the mapping technique after "marking" males with radio-transmitters. We subsequently discovered that males had 2-4 favored peripheral areas from which they sang, in what proved to be much larger territories. Our subsequent estimate of the number of males, reduced by about two-thirds, approximated the number of active nests on the tract.

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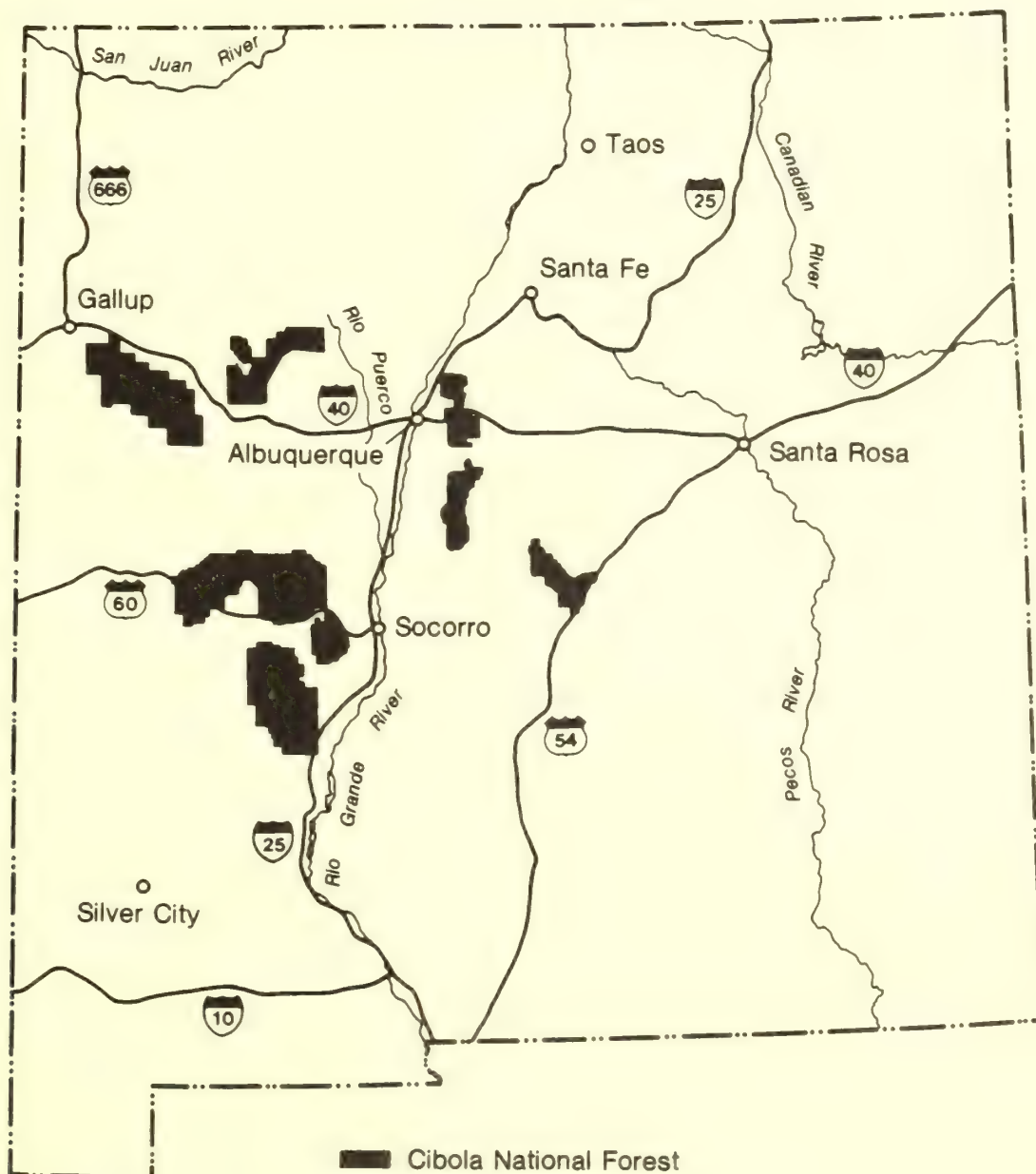
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General Technical
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A Classification of Forest Habitat Types of the Northern Portion of the Cibola National Forest, New Mexico

Billy G. Alexander, Jr.,
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Frank Ronco, Jr.,
and,
John A. Ludwig



Abstract

Vegetational data were collected from 124 sample plots on the Cibola National Forest, New Mexico, to develop a forest habitat classification based on potential natural vegetation. The 21 habitat types identified represent six climax forest series: *Picea engelmannii*, *Abies lasiocarpa*, *Picea pungens*, *Abies concolor*, *Pseudotsuga menziesii*, and *Pinus ponderosa*. A habitat type key is included for field identification. Each habitat type is described by vegetational composition, topographical occurrence, and related and adjacent habitats.

Acknowledgment

The authors thank Mr. J. S. Kirkpatrick and the administrators of the Elena Gallegos Grant for providing access to undisturbed sites on the Sandia Escarpment.

A Classification of Forest Habitat Types of the Northern Portion of the Cibola National Forest, New Mexico¹

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INTRODUCTION

The forests of the Cibola National Forest cover extensive areas with diverse vegetation. Classifying and defining vegetational units within the diverse forest ecosystem is important to forest resource management planning and its application. A classification is a basis for communication among land managers about vegetational responses to ecological changes.

Many previous studies of vegetational composition in the southwestern United States have been descriptive, but have not been comprehensive (Merkle 1954, Moir 1967, Hanks and Dick-Peddie 1974, Dye and Moir 1977). Other studies concentrated on classification systems with limited application because they described only broad vegetational units (Donart et al. 1978, Layser and Schubert 1979).

Moir and Ludwig (1979) took the first step towards a regional forest habitat type classification. Their study classified the mixed conifer and spruce-fir forests of Arizona and New Mexico and provided a guide for further studies of other forest series. Hanks et al. (1983) classified forest habitat types for the *Pinus ponderosa* series in Arizona. Alexander et al. (1984b) expanded the classification for the *Pseudotsuga menziesii* series in Arizona. Other studies classified the following National Forests: Lincoln (Alexander et al. 1984a); Apache, Cibola (Magdalena District only), and Gila⁵; Carson, Santa Fe, San Juan, and parts of the Rio Grande and San Isabel (DeVelice et al. 1986). Field work also is in progress to develop classifications for the Coronado, Prescott, and Tonto National Forests in Arizona.⁶

The terminology used in this paper follows Daubenmire (1968). A plant association is the plant community representing potential natural vegetation, which is the climax vegetation on a site resulting from natural succession. All areas that are capable of supporting the same plant association are termed a habitat type (HT), and a phase (P) is a classification level that retains overstory and undergrowth characteristics of habitat types, but differs uniformly and predictably in minor vegetational and site components.

Climax vegetation is the assemblage of plant abundance and composition in equilibrium with the environment

⁵Fitzhugh, E. Lee, William H. Moir, John A. Ludwig, and Frank Ronco, Jr. Forest habitat types in the Apache, Gila, and part of the Cibola National Forests. Manuscript in preparation. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

⁶Forest habitat type classification on these Forests is now being conducted under cooperative agreement with New Mexico State University, with supervision provided by the Rocky Mountain Station's Research Work Unit in Flagstaff, Ariz.

in the absence of disturbance. An edaphic climax can occur where soil types and conditions are the primary influences on vegetation composition, and topographic climaxes occur where topography is the primary influence. Where topography also affects soil development, the combined effect results in a topo-edaphic climax. The vegetation of climax sites where soils and topography are of a secondary influence are called climatic climax, where climate is the primary influence.

Recurring disturbances can create shifts in plant equilibriums resulting in changes in abundance and composition, and the establishment of disclimax vegetation. A common disclimax, with specific species composition, is maintained by repetitive fire.

STUDY AREA

The Cibola National Forest is in north-central New Mexico (fig. 1). The administrative units covered by this study include the Mount Taylor, Sandia, and Mountainair Ranger Districts. However, no plots suitable for developing a classification were found in the Gallinas Mountains of the Mountainair District. The Magdalena Ranger District, at the southern end of the Forest, was not sampled because it was included in a previous study involving the Gila and Apache National Forests⁵. The Ranger Districts are not contiguous; the study area is fragmented into several mountain ranges, including the San Mateo Mountains, Zuni Mountains, Sandia Mountains, and Manzano Mountains (fig. 2).

The San Mateo Mountains referred to in this study are those northeast of Grants, New Mexico, and include Mount Taylor which, rising to over 11,000 feet (3,350 m), is the highest peak. Another range, also known as the San Mateo Mountains, is on the Magdalena District. The Zuni Mountains, west and southwest of Grants, are lower, reaching just over 9,200 feet (2,800 m). The Oso Ridge of the Zuni Mountains form the Continental Divide in this area. The Sandia Mountains, east of Albuquerque, form the abrupt Sandia Crest, which is a large west-facing escarpment rising to over 10,500 feet (3,200 m). The Manzano Mountains are southeast of Albuquerque, with elevations over 9,300 feet (2,835 m).

The Mount Taylor region encompasses the largest volcanic field in the study area; parent materials are primarily basaltic. This field consists of a series of mesas, including Horace Mesa, Jara Mesa, and Mateo Mesa. The southeast portion of the Zuni Mountains is also the site of a volcanic field where cinder soils are prevalent. Flows of old malpais or lava also are found in this region. The

remainder of the Zuni Mountains has been uplifted by granitic rocks extruded through strata of limestones, siltstones, sandstones, and shales (Williams 1967). The Sandia Crest and the Manzano Mountains also are uplifts. The overlying limestones and siltstones have remained intact, resulting in less granitic and gneissic parent materials.

The climate of the Cibola National Forest is continental, with two wet and two relatively dry periods. During the winter (December through March), precipitation is mostly snow resulting from large Pacific Coast frontal storms. During the summer (July through September), large convectional thunderstorms account for the precipitation, with moisture derived from air masses originating in the Gulf of Mexico. The spring and fall months are relatively dry. In the Mount Taylor Ranger District, 22–33% of the annual rainfall is in the winter; 41–50% is in the summer (Williams 1967). Precipitation patterns are similar for the Sandia and Mountainair Ranger Districts (Bourlier et al. 1970). Temperature for this region varies widely, both seasonally and daily; daily variation in winter may be as much as 75° F (24° C).

Throughout the Southwest, mountain ranges are isolated, with desert or grassland intervening, and are characterized as biogeographical islands. Much of the diversity in plant communities is a result of the wide differences in topography in the area. The monocline forming the Oso Ridge of the Zuni Mountains results in cool, moist canyons along its southwestern slope. The topographical relief of Mount Taylor supports several different plant communities, including the spruce-fir forests

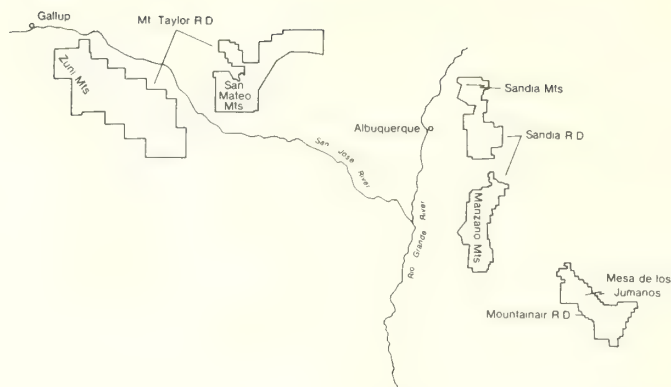


Figure 2.—Ranger Districts and major mountain ranges covered by the study. The Magdalena Ranger District of the Cibola National Forest was classified in earlier work.

at elevations of over 10,000 feet (3,050 m). The west slope of the Sandia Escarpment is dissected by steep drainages that provide unusual sites for certain *Abies concolor* and *Pinus ponderosa* habitat types. The long, east slope of the Sandia Mountains supports vast spruce-fir forests near the uppermost elevations, gradually changing to other forest series as elevation decreases, eventually terminating in pinyon-juniper woodlands. The Manzano Mountains support similar vegetation.

METHODS

FIELD SAMPLING

Procedures for sampling forest stands followed those of Daubenmire (1968), as modified by Moir and Ludwig (1983). Before field work began, people with knowledge of the Cibola National Forest were contacted for information on locations of mature stands. Aerial photographs, fire occurrence maps, and historical information were studied before field sampling. After on-site inspection, forest stands were subjectively selected using the following criteria: (1) a mature, self-reproducing tree canopy, (2) an undergrowth that had recovered from past disturbance (determined by the absence of plants and physical signs indicative of disturbance), and (3) a homogeneous stand that was not an ecotone between two distinctly different plant associations.

Data from selected stands were collected using one of three sampling methods: reconnaissance, analytical, and validation. The reconnaissance method was a quick and efficient sampling method compared to the detailed analytical plot method. Validation plots documented the presence of known habitat types and were similar to, but less detailed than, reconnaissance and analytical plots. Validation plots were used in the analysis of vegetation characteristics in the same manner as reconnaissance plots. The decision to use validation plots was based on whether the habitat type represented by the stand could be defined by an existing habitat type classification in the region.

Reconnaissance plots were circular (35.8 feet or 10.9 m radius) and covered 4,037 square feet (375 m²). Canopy coverage for each undergrowth species was visually

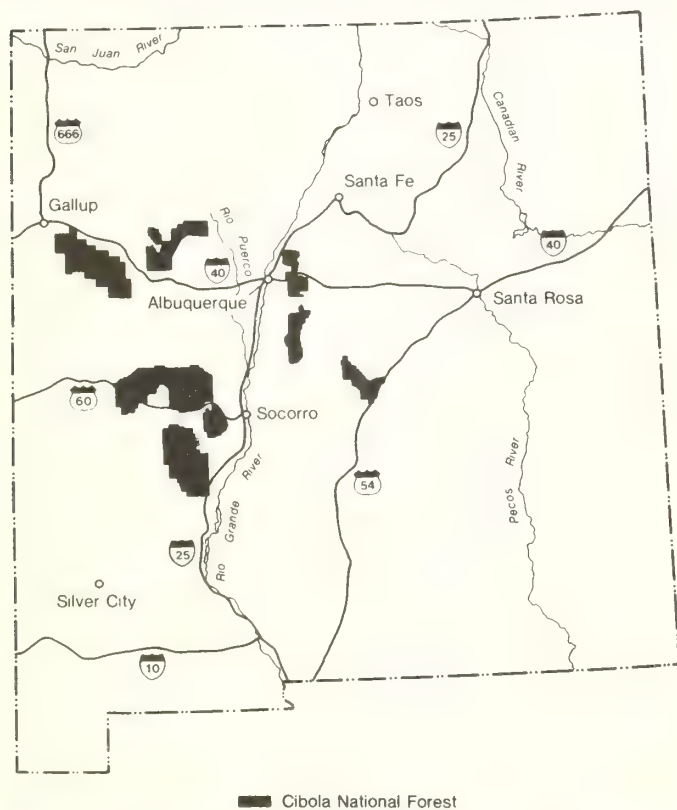


Figure 1.—Location of the Cibola National Forest in the state of New Mexico.

estimated to the nearest percent. Trees were placed in the following size categories: (1) seedlings—up to 4.5 feet (1.37 m) tall, (2) small saplings—4.5 feet (1.37 m) tall to 2 inches (5.1 cm) diameter at breast height (d.b.h.), (3) large saplings/poles—2 to 10 inches (5.1 to 25.4 cm) d.b.h., and (4) mature trees—greater than 10 inches (25.4 cm) d.b.h. A prism tally was used to determine basal area. Basal area is reported in discussions of certain habitat types where it may help in identification. Because of sample size and the nonrandom nature of data collection, basal area figures should not be used to compare productivity for habitat types. Validation plots were identical to reconnaissance plots in size and data collection methods, with the exception that timber data and much of the abiotic data were not collected.

One analytical plot, 49.2 by 82.0 feet (15 by 25 m), was established for about every 10 reconnaissance plots. Both types of plots provided essentially the same information. In the analytical plots, two transect lines, 16.4 feet (5 m) apart, were placed parallel to the long axis, and 25 rectangular quadrats (7.9 by 19.7 inches or 20 by 50 cm) were spaced at 3.3-foot (1 m) intervals along each transect. Plant cover estimates were recorded in percentage coverage classes according to Moir and Ludwig (1983). The primary function of analytical plots was to provide calibration between visual estimates of reconnaissance and validation plots and the more precise measurements obtained from analytical quadrats. Also, calibration narrowed differences in estimates of cover values between investigators so that data would be comparable. To aid calibration, a reconnaissance plot always was visually estimated first on the same site where an analytical plot was measured. Results of the two methods were compared before leaving the site, and discrepancies were adjusted after further examination.

Abiotic data included location, aspect, slope, elevation, landform, and topographic position (ridge, upper slope, midslope, lower slope, bench, and streamside). The soil surface was described according to the percentage of exposed rocks, mineral soil, litter, moss and lichen, and vascular plant basal area. Evidence of historical disturbance, such as fire frequency, logging, and grazing influence, also was recorded.

DATA ANALYSIS

Initially, plots were subjectively grouped into climax forest series according to the dominant overstory species and reproduction. Within a series, individual plots were grouped according to similarities in species composition. Successive refinement was based on relevé tables—data matrices with coverage values of species in each plot (Becking 1957). Constancy was an important element determining the reliability of a species to represent a given type of habitat type. Groupings were further clarified by analyzing the total number of species in the plots, historical data, and abiotic features. Subsequent data analysis used ordination (principal component analysis) to increase objectivity, learn more about the interaction of species, substantiate earlier judgments, or

reveal types not previously defined (Moir and Ludwig 1983). The process of iterative group refinement, using subjective and analytical computer procedures, was continued until stands were separated into representative units with relatively consistent site characteristics and similar tree, shrub, forb, and graminoid components. When appropriate, these units, or habitat types, were further categorized by phases. Names of habitat types were coordinated with other studies in the Southwest. Scientific names of plants follow the synonymy adopted by Fitzhugh et al.⁵ (Appendix B) and common names are from Nickerson et al. (1976).

RESULTS AND DISCUSSION

The habitat types and phases of the studied portion of the Cibola National Forest are shown in table 1, and a key to their identity is in Appendix A. Six forest series are found on the Cibola National Forest: *Picea engelmannii*, *Abies lasiocarpa*, *Picea pungens*, *Abies concolor*, *Pseudotsuga menziesii*, and *Pinus ponderosa*.

Identification of 18 habitat types or phases, except for some that are common or well distributed in the study area, was based on a limited sample size consisting of less than five plots (table 1). In six instances, the small sample size resulted from the scarcity of habitat types in the study area and the difficulty in locating suitable stands in which to establish plots. Few plots were measured in the remaining 12 habitat types, merely documenting those previously identified by others, in order to concentrate sampling efforts on unknown habitat types.

Descriptions of habitat types were based on a combination of data collected from this study and information included in other classifications where sampling was more comprehensive. The classifications utilized for this purpose are those that have been developed for (1) the Apache and Gila National Forests and the Magdalena District of the Cibola National Forest⁵, (2) the Lincoln National Forest (Alexander et al. 1984a), (3) the Colorado Plateau (Alexander et al. 1984b, Hanks et al. 1983), and (4) northern New Mexico and southern Colorado (DeVelice et al. 1986). The classification by Moir and Ludwig (1979) for spruce-fir and mixed conifer forests in Arizona and New Mexico also was used.

Habitat type names were standardized to ensure regional compatibility between classifications. An important exception to nomenclature standardization involved name changes of habitat types previously identified by Moir and Ludwig (1979). More intensive sampling of habitat types since their publication suggested that *Pseudotsuga menziesii* does not always attain the coclimax position in stands of *Abies concolor* forest series that was previously believed. For this reason and purposes of standardization, *Pseudotsuga menziesii* has been deleted from the names of several *Abies concolor* habitat types. Types that previously were identified by Moir and Ludwig (1979) as "*Abies concolor*-*Pseudotsuga menziesii*..." are now "*Abies concolor*..." This should be kept in mind when comparing the two classifications.

Table 1. List of Habitat Types and Phases on the Cibola National Forest, except the Magdalena District.

HABITAT NAME	ABBREVIATION	NUMBER OF PLOTS
<i>Picea engelmannii</i> series		
<i>Picea engelmannii</i> /moss habitat type	PIEN/MOSS HT	2
<i>Abies lasiocarpa</i> series		
<i>Abies lasiocarpa</i> / <i>Acer glabrum</i> habitat type	ABLA/ACGL HT	3
<i>Abies lasiocarpa</i> / <i>Erigeron eximius</i> habitat type	ABLA/EREX HT	7
<i>Abies lasiocarpa</i> / <i>Vaccinium myrtillus</i> habitat type	ABLA/VAMY HT	1
<i>Picea pungens</i> series		
<i>Picea pungens</i> / <i>Carex foenea</i> habitat type	PIPU/CAFO HT	3
<i>Picea pungens</i> / <i>Cornus stolonifera</i> habitat type	PIPU/COST HT	4
<i>Abies concolor</i> series		
<i>Abies concolor</i> / <i>Acer glabrum</i> habitat type	ABCO/ACGL HT	
<i>Acer glabrum</i> typic phase	ACGL typic P	3
Riparian phase	RIPARIAN P	3
<i>Berberis repens</i> phase	BERE P	5
<i>Abies concolor</i> / <i>Quercus gambelii</i> habitat type	ABCO/QUGA HT	14
<i>Pseudotsuga menziesii</i> series		
<i>Pseudotsuga menziesii</i> / <i>Bromus ciliatus</i> habitat type	PSME/BRCI HT	2
<i>Pseudotsuga menziesii</i> / <i>Festuca arizonica</i> habitat type	PSME/FEAR HT	4
<i>Pseudotsuga menziesii</i> / <i>Muhlenbergia montana</i> habitat type	PSME/MUMO HT	5
<i>Pseudotsuga menziesii</i> / <i>Quercus gambelii</i> habitat type	PSME/QUGA HT	2
<i>Pinus ponderosa</i> series		
<i>Pinus ponderosa</i> / <i>Quercus gambelii</i> habitat type	PIPO/QUGA HT	
<i>Quercus gambelii</i> typic phase	QUGA typic P	5
<i>Pinus edulis</i> phase	PIED P	12
<i>Schizachyrium scoparium</i> phase	SCSC P	5
<i>Pinus ponderosa</i> / <i>Festuca arizonica</i> habitat type	PIPO/FEAR HT	
<i>Festuca arizonica</i> typic phase	FEAR typic P	15
<i>Bouteloua gracilis</i> phase	BOGR P	2
<i>Quercus gambelii</i> phase	QUGA P	2
<i>Pinus ponderosa</i> / <i>Muhlenbergia virescens</i> habitat type	PIPO/MUVI HT	3
<i>Pinus ponderosa</i> / <i>Muhlenbergia virescens</i> - <i>Festuca arizonica</i> habitat type	PIPO/MUVI-FEAR HT	1
<i>Pinus ponderosa</i> / <i>Muhlenbergia montana</i> habitat type	PIPO/MUMO HT	11
<i>Pinus ponderosa</i> / <i>Bouteloua gracilis</i> habitat type	PIPO/BOGR HT	4
<i>Pinus ponderosa</i> /Cinder soils habitat type	PIPO/CINDER HT	4
<i>Pinus ponderosa</i> /Riparian habitat type	PIPO/RIPARIAN HT	1
<i>Pinus ponderosa</i> /Rockland habitat type	PIPO/ROCKLAND HT	1

Each habitat type description begins with a discussion of diagnostic vegetation characterizing that type.⁷ Overstory tree species are described in relation to their climax and successional roles within the habitat type, and undergrowth plant species most consistently present or absent in the habitat type are labeled "diagnostic." Other plants that are not as important as diagnostic species also are discussed if they provide clues to field identification of the habitat type. Coverage values reported in the text are based on plot averages.

A general topographical description is included in the habitat type description. However, because environmental factors may be interactive and compensating, several different topographical locations may support the same habitat type. In contrast, there are situations where a habitat type may be restricted to a particular set of topographical conditions; for example, the *Picea pungens*/*Cornus stolonifera* habitat type is confined to streamside

⁷Taxonomic references were Lehr (1978), Lehr and Pinkava (1980, 1982), Martin and Hutchins (1980), and Weber and Johnston (1979).

benches. The habitat type descriptions also include discussions of adjacent habitat types and ecotones. A discussion section concludes the description of each habitat type and provides additional information gathered during the course of the study.

SPRUCE-FIR HABITAT TYPES

Picea engelmannii Series

Picea engelmannii/Moss habitat type (PIEN/MOSS HT; Engelmann spruce/moss)

Vegetation.—*Picea engelmannii* is dominant in the overstory, with mature *Abies lasiocarpa* less numerous (fig. 3). Regeneration of these two species may be abundant. *Populus tremuloides* is the major successional species present. A diagnostic feature of this habitat type

is the sparse undergrowth, which rarely exceeds 3% cover. *Vaccinium myrtillus* may be present, but usually in trace amounts. Graminoids often are absent, but *Bromus ciliatus* sometimes is present. Forbs rarely exceed 1% cover. Common species include *Aquilegia chrysantha*, *Erigeron eximius*, *Lathyrus arizonicus*, *Smilacina stellata*, and *Ramischia secunda*.

The prominent ground cover in the PIEN/MOSS HT is a thick litter layer, with mosses or lichens occurring in patches. Cover by such plants is usually about 10% but can exceed 30%.

Physical setting.—The PIEN/MOSS HT occurs in the Mount Taylor area near the top of mountain ridges, often the summit or peak. It is found on gentle or nearly flat slopes on north aspects. Elevations range from 10,500 to 11,000 feet (3,200 to 3,350 m).

Ecotones and adjacent habitats.—On Mount Taylor, the PIEN/MOSS HT is upslope from the *Abies lasiocarpa*/*Vaccinium myrtillus* habitat type, which is found on much steeper slopes. The PIEN/MOSS HT often is adjacent to large, open meadows of *Danthonia parryi* found in the Mount Taylor area.

Discussion.—The PIEN/MOSS HT is at the cold end of the temperature gradient for spruce-fir forests, making it one of the coldest forest habitat types on the Cibola National Forest. Within the study area, it is restricted to the Mount Taylor area.

Site disturbance results in drastic successional changes in plant composition in this habitat type. Complete overstory removal increases the shrub and graminoid layers. Species of *Ribes* and *Rubus* dominate disturbed sites. Among abundant graminoids, *Carex* and *Cyperus* are common. Common seral forbs include *Cirsium* spp., *Lathyrus arizonicus*, *Lupinus* spp., and *Vicia americana*. *Populus tremuloides* is a colonizing overstory species, with *Pseudotsuga menziesii* becoming established later. These two species provide the cooler microsite conditions necessary for establishing an understory of *Picea engelmannii* and *Abies lasiocarpa*. The high light intensity and warmer conditions of the exposed sites may

restrict the establishment of these two species (Ronco 1970).

The PIEN/MOSS HT is a common habitat type of the spruce-fir forests of the Southwest (Moir and Ludwig 1979). It has been observed on higher mountain summits in the Gila National Forest⁵. The dense canopy cover and the more gentle slopes of this habitat type result in snow retention late into the spring.

Although sample size (N = 2) was small, species composition and relative abundance in the sampled plots correlated well with that found by Moir and Ludwig (1979) and by others in the Apache and Gila National Forests.⁵

Abies lasiocarpa Series

Abies lasiocarpa/*Acer glabrum* habitat type (ABLA/ACGL HT; subalpine fir/Rocky Mountain maple)

Vegetation.—*Abies lasiocarpa* is the dominant timber species of this habitat type (fig. 4). *Picea engelmannii* is relatively less abundant than on other *Abies lasiocarpa* series habitat types. *Pseudotsuga menziesii* and *Abies concolor* are major late-successional species, and often are present as decadent individuals in the young climax forest. *Populus tremuloides* is the major early seral species, providing the protective canopy under which mixed conifers become established.

Acer glabrum is the dominant shrub species, often occurring in tree form and dominating a portion of the lower canopy. *Symphoricarpos oreophilus* also is common. Total shrub cover averages over 10%. *Bromus ciliatus* dominates the grass cover, with coverage values as high as 60%. *Festuca sororia* is often associated with *Bromus ciliatus*. Average grass cover sampled was about 20%. *Erigeron eximius* occurs only in association with *Acer glabrum* and *Bromus ciliatus*. Other common forbs include *Aquilegia elegantula* and *Lathyrus arizonicus*. Average forb cover was over 10%.



Figure 3.—*Picea engelmannii*/Moss habitat type: La Mesa Peak (10,720 feet or 3,270 m). *Picea engelmannii* dominates the canopy, with occasional *Abies lasiocarpa*. Total shrub, grass, and forb cover is less than 5%.



Figure 4.—*Abies lasiocarpa*/*Acer glabrum* habitat type: Sandia Crest above Osha Spring (9,980 feet or 3,040 m). *Abies lasiocarpa* dominates the canopy but *Pseudotsuga menziesii* is abundant. *Acer glabrum* grows into canopy and is prominent on the site.

Physical setting.—The ABLA/ACGL HT was found only on the long easterly slope of the Sandia Mountains. It may occur in the Manzano Mountains, although no stands were sampled there. This type occurs between 9,700 and 10,000 feet (2,955 and 3,050 m) on northeast aspects with slopes ranging between 15% and 45%. Litter cover is high, and the soils have a well-developed layer of partially decomposed organic matter.

Ecotones and adjacent habitats.—The ABLA/ACGL HT represents the lowest elevational habitat type of the spruce-fir forests sampled in the study area. It is transitional to the ABCO/ACGL mixed conifer habitat type along its lower elevational boundary, as indicated by the prominent role of *Pseudotsuga menziesii* in the late successional stages of the ABLA/ACGL HT. The ABLA/EREX HT occurs along its higher elevation border.

Discussion.—Sample size ($N = 3$) for this study was small because of limited extent of this type on the Cibola National Forest. The ABLA/ACGL HT probably is closely related to the *Picea engelmannii*/*Acer glabrum* habitat type described earlier by Moir and Ludwig (1979). However, the ABLA/ACGL HT differs in that it may be found over a broad range of topographical situations, whereas the PIEN/ACGL HT is restricted to canyons at relatively low elevations. Although the ABLA/ACGL and PIEN/ACGL HT's exhibit similarities in undergrowth characteristics, the overstories are strikingly different. Few mature *Picea engelmannii* trees are found in stands representing the ABLA/ACGL HT.

Populus tremuloides completely dominates this habitat type during successional stages following major disturbances. *Pseudotsuga menziesii* and *Abies concolor* slowly become established and crowd aspen from the site. Finally, *Abies lasiocarpa* and *Picea engelmannii* regenerate under the 50- to 100-year-old mixed conifer canopy and eventually dominate the stand.

As with other high elevation types, the ABLA/ACGL HT is an important watershed habitat type, and because of the great diversity in shrub and herbaceous layers, it also is important summer habitat for wildlife. Water production and wildlife may benefit from small patchy-sized openings in the canopy.

***Abies lasiocarpa*/Erigeron eximius habitat type (ABLA/EREX HT; subalpine fir/forest fleabane)**

Vegetation.—*Abies lasiocarpa* and *Picea engelmannii* are the dominant timber species in this habitat type (fig. 5). There may, however, be an inverse relationship between abundance of the two species related to stand density; *Abies lasiocarpa* appears to dominate dense stands; *Picea engelmannii* is more abundant in open stands. The successional relationship between these two species is not clear for this habitat type. *Pseudotsuga menziesii* and *Abies concolor* are present as late successional elements, but rarely as mature trees in older stands. *Populus tremuloides* is the major early seral tree species.

Vaccinium myrtillus is absent from this type, but *Symphoricarpos oreophilus* and *Berberis repens* are common. Shrub cover is low, averaging less than 2%. Mean grass cover is 8%, but increases in openings of the forest



Figure 5.—*Abies lasiocarpa*/Erigeron eximius habitat type: La Mosca Canyon (9,620 feet or 2,930 m). *Abies lasiocarpa* and *Picea engelmannii* are codominant, with scattered *Pseudotsuga menziesii*. *Erigeron eximius* and *Vicia americana* are prominent, but the shrub and grass layers are minimal.

canopy. Common graminoid species are *Bromus ciliatus* and *Carex foenea*. Frequent, but less common grasses include: *Danthonia parryi*, *Festuca arizonica*, *Festuca thurberi*, and *Trisetum montanum*.

Erigeron eximius is a constant forb species. *Aquilegia elegantula*, *Lathyrus arizonicus*, *Osmorhiza depauperata*, and *Pseudocymopterus montanus* are common. In stands where *Populus tremuloides* is abundant, *Lathyrus arizonicus* and *Vicia americana* cover can exceed 20%. Total forb cover is normally 15–20%.

Physical setting.—The ABLA/EREX HT is found throughout the Cibola National Forest on ridge slopes and uplands with 5–60% slopes. This type can be found on all aspects from 10,000 to 10,900 feet (3,050 to 3,320 m) elevation. One stand was found at a lower elevation, 9,600 feet (2,925 m), on a lower canyon slope. However, it was not determined whether this habitat type occurs at such low elevations in canyons throughout the forest. Moir and Ludwig (1979) reported the *Abies lasiocarpa*/Erigeron superbus⁸ habitat type as occurring on canyon benches and streamside sites.

Ecotones and adjacent habitats.—The ABLA/EREX HT borders the *Abies lasiocarpa*/*Vaccinium myrtillus* habitat type or high elevation meadows along its upper borders. Where the type abuts open areas—particularly the high meadows of Mount Taylor—the grass component may be abundant, decreasing as the canopy density increases. In the Sandia Crest area, the ABLA/EREX HT borders the *Abies lasiocarpa*/*Acer glabrum* habitat type at lower elevations.

Discussion.—The ABLA/EREX HT is widespread on the Cibola National Forest, and it also is a common habitat type of the spruce-fir forests in Arizona and New Mexico (Moir and Ludwig 1979, Alexander et al. 1984a, DeVelice et al. 1986, Fitzhugh et al.⁹). Stands in the Cibola National Forest occur at higher elevations than those described for the other areas. Mean basal area for timber species was 217 square feet per acre (49.9 m²/ha).

⁸*Erigeron superbus* and *E. eximius* are synonymous (see Appendix B), and the latter is considered the acceptable name in habitat classifications in the Southwest.

The rich herbaceous undergrowth and interspersed patches of seral *Populus tremuloides* provide important summer habitat for wildlife. Such interspersed habitat may be maintained by fire or silvicultural practices which open the canopy. The ABLA/EREX HT also is an important watershed habitat type, because it retains snowpack late into the spring.

***Abies lasiocarpa*/Vaccinium myrtillus habitat type (ABLA/VAMY HT; subalpine fir/Rocky Mountain whortleberry)**

Vegetation.—The overstory of the ABLA/VAMY HT is dominated by *Abies lasiocarpa* and *Picea engelmannii* (fig. 6). Regeneration often is equally divided between the two species. *Abies concolor* and *Pseudotsuga menziesii* are absent from older stands even though they sometimes attain minor successional importance in the type. *Populus tremuloides* is the major species during early succession.

Vaccinium myrtillus is the dominant shrub in this habitat type; its cover ranges from a trace to over 40% in sampled plots. Moir and Ludwig (1979) found the mean cover for *Vaccinium* in the ABLA/VAMY HT to be over 60%. They also found that common grasses include *Bromus ciliatus* and *Trisetum montanum*, but grasses often are sparse or absent. Consistent forbs are *Erigeron eximius*, *Lathyrus arizonicus*, and *Ramischia secunda*. Although *Erigeron eximius* is common in this habitat type, it always occurs in association with *Vaccinium myrtillus*.

Physical setting.—Within the study area, the ABLA/VAMY HT was found only at upper elevations of Mount Taylor on north to northwest aspects. Sites were situated on high ridges between 10,000 and 10,800 feet (3,050 and 3,290 m) elevation. The type occurs in some localities on slopes that are steeper than 60%. Litter layers are thick, and moss is often present.

Ecotones and adjacent habitats.—Stands of the ABLA/VAMY HT were found adjacent to the PIEN/



Figure 6.—*Abies lasiocarpa*/Vaccinium myrtillus habitat type: La Mosca Peak (10,550 feet or 3,215 m). *Abies lasiocarpa* is abundant, with *Picea engelmannii* codominant. *Vaccinium myrtillus* often covers more than 25% of the ground surface; other species are not abundant.

MOSS HT, which is situated upslope on more gentle topography. Transition to the ABLA/VAMY HT may be rapid because of rapid changes in slope. On warmer sites, the *Abies lasiocarpa*/*Erigeron eximius* habitat type is adjacent.

Discussion.—The ABLA/VAMY HT is found on steep slopes in the Mount Taylor area. The overstory canopy is more open than the PIEN/MOSS HT. Sites on which the habitat type is found are well drained, giving the type a drier appearance than the PIEN/MOSS HT.

Successional stands are dominated by shrubs, and *Vaccinium myrtillus* may be replaced by *Ribes* spp. *Populus tremuloides* dominates the seral tree canopy. Spruce and fir regenerate under the *Populus tremuloides* canopy. *Abies lasiocarpa* and *Picea engelmannii* seedlings may have a higher survival rate because of the less harsh environment on north aspects where this habitat type is usually found (Ronco 1970).

The ABLA/VAMY HT is widespread, occurring in most forests of the Southwest (Moir and Ludwig 1979, DeVelice et al. 1986, Fitzhugh et al.⁵). It was not, however, found on the Lincoln National Forest in southern New Mexico (Alexander et al. 1984a). Only one plot of the ABLA/VAMY HT was found on the Cibola National Forest, which illustrates its limited occurrence here. The one plot, however, validates the occurrence of the type because of similar characteristics with plots elsewhere (Moir and Ludwig 1979, DeVelice et al. 1986, Fitzhugh et al.⁵).

MIXED CONIFER HABITAT TYPES

Picea pungens Series

***Picea pungens*/Carex foenea habitat type (PIPU/CAFO HT; blue spruce/silvertop sedge)**

Vegetation.—*Picea pungens* and *Pseudotsuga menziesii* dominate the climax overstory and regeneration stratum of this habitat type (fig. 7). Other conifer species may be present, but vary in abundance. *Populus tremuloides* is the major successional species, often persisting into the later stages of overstory development.

Common shrubs are *Acer glabrum*, *Berberis repens*, and *Ribes* spp. Average shrub cover for the plots was 8%. *Cornus stolonifera* is often present, but showing less coverage than grasses. *Carex foenea* is abundant and dominates the undergrowth, often with cover exceeding 10%. *Festuca arizonica*, *Festuca thurberi*, and *Poa fendleriana* are all common but less abundant than *Carex foenea*. Total graminoid cover averaged 29% for the sample plots.

The forb layer is highly diverse and abundant in this habitat type. Average cover in the plots was 41%. Species of *Fragaria* are present, though not dominant in the sampled plots. Common forb species include *Achillia millefolium*, *Erigeron eximius*, *Geranium richardsonii*, *Lathyrus arizonicus*, *Pseudocymopterus montanus*, and *Vicia americana*.

Physical setting.—The PIPU/CAFO HT is restricted to cool moist canyon sideslopes. It can be found on most

aspects between 8,000 and 9,500 feet (2,440 and 2,895 m) in elevation. This elevational range may be extended if favorable microsite conditions for the habitat type are present.

Ecotones and adjacent habitats.—Adjacent habitats vary according to the canyon site occupied by the PIPU/CAFO HT. When the type occurs at higher elevations, it is adjacent to spruce-fir forests, the ABLA/EREX HT being most common. At midelevations, adjacent habitat types vary according to the aspect of the canyon slopes; warmer aspects have *Pinus ponderosa* types present; cooler aspects support *Abies concolor* types. At lower elevations, the type abuts *Pinus ponderosa* forests, commonly the *Pinus ponderosa*/*Festuca arizonica* habitat type (PIPO/FEAR HT).

Discussion.—This habitat type is found in the Zuni Mountains and the Mount Taylor area of the Cibola National Forest. The small sample size ($N = 3$) reflects its limited distribution on the Cibola. The PIPU/CAFO HT was previously identified by DeVelice et al. (1986), Moir and Ludwig (1979), and Fitzhugh et al.⁵ The nomenclature of the type follows that of Fitzhugh et al.,⁵ who separated the PIPU/CAFO HT of Moir and Ludwig (1979) into the PIPU/CAFO and PIPU/FEAR habitat types. Appendix E shows mean forb dominance in the PIPU/CAFO HT to be within the range of the *Picea pungens*/*Erigeron eximius* habitat type of Fitzhugh et al.⁵ This mean value was elevated by one plot that may have actually represented the PIPU/EREX HT, but the possibility of historical disturbance prevented conclusive separation from the PIPU/CAFO HT.

Populus tremuloides is the major successional overstory species dominating sites following disturbance. Forb and grass cover, including *Festuca arizonica* and *Poa fendleriana*, increases when the canopy opens. Heavy grazing may also increase the proportion of forbs.

Because this habitat type is cool and moist (nearly riparian) and links the two opposite slopes of the canyon, it is important for wildlife, particularly big game. The topographical conditions under which this habitat type occurs creates abrupt edges between habitat types which

are favorable for many kinds of wildlife. Evidence of grazing by wildlife and domestic stock was observed in this habitat type.

***Picea pungens*/Cornus stolonifera habitat type (PIPU/COST HT; blue spruce/red osier dogwood)**

Vegetation.—*Picea pungens* and *Pseudotsuga menziesii* are dominant in the climax overstory and as reproduction (fig. 8), but other conifer species were absent from sample plots in this habitat type. Occasional establishment of *Juniperus osteosperma* and *J. scopulorum* may occur where adjacent habitat types are much drier. *Populus tremuloides* is abundant as the early successional tree species and persists into the later stages of the stand development.

Cornus stolonifera is the dominant shrub species, often forming dense thickets covering 20% or more of a plot. *Berberis repens* and *Pachistima myrsinites* are constant species with coverage ranging from 1% to 5%. Other common shrubs include *Acer glabrum*, *Alnus tenuifolia*, *Lonicera involucrata*, *Quercus gambelii*, *Ribes* spp., *Salix* spp., and *Symphoricarpos oreophilus*. Shrubs are the dominant undergrowth component of this habitat type, showing an average cover of over 45%.

Graminoids are subordinate to shrubs with *Carex foenea* sometimes abundant, but if so, always associated with *Cornus stolonifera*. *Bromus ciliatus* and *Carex rossii* also are common. Forbs are subordinate to the shrub layer. Average cover of forbs is 17% for the samples. *Achillea millefolium*, *Lathyrus arizonicus*, *Mertensia franciscana*, *Smilacina racemosa*, *Thalictrum fendleri*, and *Vicia americana* are common.

Physical setting.—The PIPU/COST HT is restricted to canyons, streambanks, or slightly elevated benches. Water, either from perennial streams or subsurface sources, appears to be a requirement for this habitat type. It can be found between 7,500 and 8,500 feet (2,285 and 2,590 m) in elevation, but may extend outside this range if suitable water and topographic conditions are present. This type



Figure 7.—*Picea pungens*/*Carex foenea* habitat type: Little Water Canyon (8,240 feet or 2,510 m). *Picea pungens* and *Pseudotsuga menziesii* dominate the canopy. *Carex foenea* is the dominant graminoid with about 20% coverage. Forbs are diverse.



Figure 8.—*Picea pungens*/*Cornus stolonifera* habitat type: East Fork Water Creek (8,200 feet or 2,500 m). *Picea pungens* is codominant with *Pseudotsuga menziesii*. *Cornus stolonifera* is the dominant low shrub.

may be found on canyon slopes, but such stands usually are ecotones.

Ecotones and adjacent habitats.—Adjacent habitat types may vary greatly because of topographic conditions under which the PIPU/COST HT occurs. The *Pinus ponderosa*/*Festuca arizonica* habitat type is commonly found adjacent to the PIPU/COST HT in lower elevation canyons; the ABCO/QUGA HT is associated with the type at higher elevations. Adjacent habitats vary according to the aspect of canyon slopes on which they are located. Warmer aspects favor *Pinus ponderosa* series habitat types; cooler aspects support *Abies concolor* or *Pseudotsuga menziesii* series habitat types.

Discussion.—The small sample size ($N = 4$) for the PIPU/COST HT reflects the limited nature of *Picea pungens* stands on the Cibola National Forest. The unusual characters which describe this stand probably warrant separate habitat type status, despite the small sample size upon which it is based. More study on *Picea pungens* stands in this Forest probably will identify additional stands representing the PIPU/COST HT. The PIPU/COST HT is found in the Zuni Mountains, along cool canyons associated with Oso Ridge. This is a newly described *Picea pungens* habitat type for southwestern forests. It is associated with surface or subsurface water. The shrub layer is three times as dense as the forb or grass components. Moir and Ludwig (1979) recognized phases of a *Picea pungens*-*Pseudotsuga menziesii* habitat type that were dominated by low shrubs—*Arctostaphylos uva-ursi* and *Linnaea borealis*—but none of their phases exhibited dominance by taller shrubs as in this study. Fitzhugh et al.⁵ recognized only grass and forb dominated *Picea pungens* habitat types in the Gila National Forest. Mean basal area for overstory trees in the PIPU/COST HT was 178 square feet per acre (40.8 m²/ha).

The PIPU/CAFO HT differs from the PIPU/COST HT in the relative abundance of the shrub, grass, and forb components. Within the PIPU/CAFO HT, grasses are three times as abundant as shrubs, and forbs are four times as abundant. But in the PIPU/COST HT, shrub cover is three times that of grasses and more than twice that of forbs. The PIPU/COST HT appears dependent on surface or subsurface water; the PIPU/CAFO HT is less restricted.

Wet canyon sites are crucial elements of the habitat complex of a forest because they link habitat types located on either side of the canyon. Such topographic conditions often create abrupt edges between adjacent types which have radically different plant compositions. These areas are used heavily by wildlife and provide natural fire barriers. The *Picea pungens* stands in the Zuni Mountains have received limited recreational use and are in unusually good ecological condition compared to similarly situated stands in other southwestern forests.

***Abies concolor* Series**

***Abies concolor*/*Acer glabrum* habitat type (ABCO/ACGL HT; white fir/Rocky Mountain maple)**

Vegetation.—*Abies concolor* is the dominant timber species of this habitat type, and all age classes are well



Figure 9.—*Abies concolor*/*Acer glabrum* habitat type: east slope of Sandia Escarpment (9,840 feet or 3,000 m). *Abies concolor* dominates, with *Pseudotsuga menziesii* co-climax and more numerous on successional sites. *Acer glabrum* is abundant, and dominating the shrub layer. *Bromus ciliatus* also is abundant, and forbs are diverse.

represented (fig. 9). *Pseudotsuga menziesii* is codominant, and *Pinus strobiformis* and *P. ponderosa* are common. *Populus tremuloides* is the major successional species. There is a basic difference within the overstory between phases of this habitat type. Only *Abies concolor* is present in the riparian phase, while a mixture of the above species occurs in the typic and *Berberis repens* phases. *Acer negundo* is sometimes found along streamsides in the overstory of the riparian phase.

Acer glabrum is the dominant shrub species within this habitat type. *Quercus gambelii* is common in all phases, and average shrub cover is 38%. The grass component is less important than in other types, averaging 9% cover. The forbs are diverse, and sometimes form a dense cover blanketing the ground.

***Acer glabrum* (ACGL) typic phase.**—The typic phase is dominated by *Acer glabrum* in the shrub layer. *Quercus gambelii* occurs from trace amounts to over 5% cover. *Bromus ciliatus* is a common graminoid and can be abundant. Common forbs include *Achillia millefolium*, *Heuchera parviflora*, *Mertensia franciscana*, *Osmorhiza depauperata*, *Valeriana capitata*, and *Vicia americana*.

Riparian phase.—The riparian phase is distinguished by the absence of conifers, other than *Abies concolor*, in the overstory; high shrub cover and restriction to stream-side canyon bottoms are also characteristic. *Acer glabrum* can be found with over 50% cover, and *Jamesia americana* is abundant. *Quercus gambelii* is variable, but can have 10% or higher cover. *Symphoricarpos oreophilus* also is abundant. Graminoids are greatly reduced in comparison with other phases; *Bromus ciliatus* is the only consistent species. Forbs are not as dominant as shrubs on these sites, and cover is usually less than 10%. However, in one plot *Osmorhiza depauperata* had 40% cover, and the shrub layer, described above, covered the entire plot. Other common forbs include *Clematis pseudoalpina*, *Fragaria americana*, *Malaxis soulei*, *Polemonium foliosissimum*, *Senecio eremophilus*, and *Thalictrum fendleri*.

Berberis repens (BERE) phase.—The shrub layer of the BERE phase has less *Acer glabrum* and more *Quercus gambelii* than that of the typic phase. *Quercus gambelii*, however, does not exceed 10% cover. *Berberis repens* is constant, and ranges from 1% to 10% cover. *Bromus ciliatus* is a common grass. Forbs often dominate the undergrowth on these sites. *Clematis ligusticifolia* can be dominant in this phase, with over 25% cover. Common forbs include *Artemisia franserioides*, *Fragaria americana*, *Haplopappus parryi*, *Malaxis soulei*, *Polemonium foliosissimum*, *Pseudocymopterus montanus*, *Stellaria longifolia*, and *Thalictrum fendleri*.

Physical setting.—The typic phase occurs from 8,000 to 9,500 feet (2,440 to 2,895 m) on north to northeasterly aspects. It can be found on ridges at high elevations and in cool drainages at lower elevations.

Stands of the *Berberis repens* phase occur from 8,100 to 10,300 feet (2,470 to 3,140 m) in elevation, on mostly northern aspects. The *Berberis repens* phase is found on ridge sideslopes, as well as cool, moist microsites at lower elevations. The phase was sampled only on the eastern slope of the Sandia Mountains, but may occur on northern aspects of Mount Taylor.

The riparian phase of the habitat type is restricted to perennial streamsides in steep-sided, deep, shady canyons, unless sites are protected and sufficiently moist to allow establishment along ephemeral drainages with year-long subsurface flows. Elevation ranges from 7,500 to 8,200 feet (2,285 to 2,500 m). All samples were taken from the west side of the Sandia Mountains, on a variety of microsite aspects. This phase can occur in canyons bisecting warm, south exposures, if conditions are moist and shady.

Ecotones and adjacent habitats.—The typic and *Berberis repens* phases of this habitat type can be found adjacent to the ABLA/ACGL HT. An increase in *Abies lasiocarpa* and *Picea engelmannii* signifies a change to a cooler, more mesic habitat type. At lower elevations, these phases form ecotones with the *Abies concolor*/*Quercus gambelii* habitat type as *Acer glabrum* disappears from the shrub layer.

The riparian phase usually is bordered by the ABCO/QUGA HT. The contrast between the two types is exemplified by the dominance of *Acer glabrum* in the ABCO/ACGL HT and an increase in conifer species in the ABCO/QUGA HT.

Discussion.—The ABCO/ACGL HT represents a transition from the ABCO/QUGA HT to types representative of spruce-fir forests. Such transition is evident on the eastern slope of the Sandia Mountains with changes in elevation. The *Berberis repens* phase is found downslope from the spruce-fir habitat types. The riparian phase is a restricted type exemplifying riparian zones in the mixed conifer forest. The *Berberis repens* phase is more extensive than the riparian phase on the Cibola National Forest.

Abies concolor and *Pseudotsuga menziesii* were moderately to heavily infected with dwarf mistletoe in many plots. Forbs and grasses increased where canopies were open. In the *Berberis repens* phase, *Robinia neomexicana* and *Populus tremuloides* invade open sites.

The ABCO/ACGL HT has been described elsewhere in the Southwest (Moir and Ludwig 1979, Alexander et al. 1984a, Fitzhugh et al.⁵). DeVelice et al. (1986) also identified the ABCO/ACGL HT in northern New Mexico, where the *Berberis repens* phase is common. Stands in the Cibola National Forest are similar to those described by the above authors, but they represent the lower elevational range of the phase. Fitzhugh et al.⁵ and Alexander et al. (1984a) recognized the *Holodiscus dumosus* phase of the ABCO/ACGL HT in the Gila and Lincoln National Forests, respectively. Moir and Ludwig (1979) suggested that the *Berberis repens* phase occurs in the northern forests of the region, while the *Holodiscus dumosus* phase occurs in southern forests.

The riparian phase of this habitat type is similar to the *Abies concolor*/*Acer grandidentatum* habitat type of the Lincoln National Forest (Alexander 1984a). However, *Acer grandidentatum* was not found in stands on the Cibola National Forest.

Because of location in stream bottoms, riparian stands are not suitable for most timber harvesting operations. Overgrazing by livestock may result in soil loss during periods of water runoff. The phase often represents a sharply delineated, cool, moist inclusion of riparian vegetation within a much drier community. Therefore, it provides important structural diversity and thermal moderation for birds and mammals. The dense three-tiered structure of herbs, shrubs, and trees makes all phases of the habitat type important to wildlife.

***Abies concolor*/*Quercus gambelii* habitat type (ABCO/QUGA HT; white fir/Gambel oak)**

Vegetation.—*Abies concolor* and *Pseudotsuga menziesii* are codominant timber species in this habitat type (fig. 10). *Abies concolor* dominates regeneration as stands mature. *P. menziesii* is a mid-successional species, becoming established earlier than *A. concolor*. *Pinus strobiformis* is minor in this habitat type in the Cibola National Forest. *Pinus ponderosa* is a major seral species; mature trees are present in older stands. *Juniperus scopulorum* is common and may indicate rocky soils.

Quercus gambelii is the dominant shrub species, and often competes with developing conifers for canopy space. Average cover for *Q. gambelii* was 10%. *Cornus stolonifera* is common, possibly because of rocky soil conditions similar to those that result in the occurrence of *Juniperus scopulorum*. *Berberis repens* and *Symphoricarpos oreophilus* also are common shrubs. Average cover for the shrub stratum is 14%. The graminoid component is sparse, with average cover about 2.5%. It is composed of ubiquitous species such as *Carex rossii*, *Muhlenbergia montana*, *Poa fendleriana*, and *Sitanion hystrix*. Forb species are equally ubiquitous, with *Thalictrum fendleri* the most common. Other forbs which are common, but lack constancy, include *Fragaria americana*, *Geranium caespitosum*, and *Lathyrus arizonicus*. Average cover for the forb layer was 2.5%.

Physical setting.—The ABCO/QUGA HT occurs on most aspects between 7,400 and 8,700 feet (2,255 to

2,650 m), representing a lower elevational range than that discussed by Moir and Ludwig (1979). This habitat type occupies a variety of topographical positions, from lower canyon sideslopes at low elevations to upper slopes near the top of ridges at higher elevations.

Ecotones and adjacent habitats.—The ABCO/QUGA HT is widespread throughout the Cibola National Forest, bordering a variety of habitats. As moisture increases and temperature decreases, the ABCO/QUGA HT adjoins the ABCO/ACGL HT with noticeable ecotones. If the moisture-temperature change is abrupt, the ABLA/VAMY HT occurs next to the ABCO/QUGA HT, although such situations are uncommon. The *Pseudotsuga menziesii*/Muhlenbergia montana habitat type is commonly found where adjacent locations are drier. *Pinus ponderosa* habitat types are sometimes present on adjacent sites, particularly where environmental conditions become abruptly drier and warmer.

Discussion.—Data for the ABCO/QUGA HT were collected from areas adjacent to the Sandia and Manzano Mountains. The Zuni Mountains and the Mount Taylor region have relatively little area occupied by this habitat type and were not sampled. The narrow transition zone between the *Pseudotsuga menziesii* series and the *Abies lasiocarpa* series on Mount Taylor allows little representation of the *Abies concolor* series.

This habitat type, although not prominent on the Cibola National Forest, is extensive in New Mexico. *Pinus ponderosa* is an important commercial species and is a successional species in this type. However, Moir and Ludwig (1979) found that *Pinus ponderosa* exhibited poor to good growth potential in this habitat type. *Pseudotsuga menziesii* also is an important mid-successional species and persists into the latter stages of stand development. Mean basal area for the timber species was 126 square feet per acre (29 m²/ha).

Festuca arizonica and *Muhlenbergia virescens* were absent from plots in the Cibola National Forest. However, both species denote respective phases of the ABCO-

PSME/QUGA HT (equivalent to the ABCO/QUGA HT) found elsewhere by Moir and Ludwig (1979). Similarly, *Holodiscus dumosus* occurred in trace amounts on three of the ABCO/QUGA HT plots in this study, but its presence is believed to be accidental and not indicative of the HODU phase found on the Lincoln National Forest (Alexander et al. 1984a).

The major disturbance affecting the ABCO/QUGA HT is fire. Dense shrub layers lead to well-developed fuel ladders and severe fires. As a consequence, *Quercus gambelii* sprouts profusely within these burned areas, and results in persistent oak stands that compete with conifers, often *Pinus ponderosa*, during stand development. *Pseudotsuga menziesii* and *Abies concolor* reproduction may be killed by low intensity fires during early successional stages, creating a disclimax of the more fire resistant *Pinus ponderosa*. However, after a few years, *Pseudotsuga menziesii*, with its thicker bark, can withstand such low intensity fires.

Some slopes supported alternate strips of pinyon-juniper, *Abies concolor*, and brushy *Quercus gambelii* stands that were oriented perpendicular to the contour of the slope, apparently reflecting fires of different intensities or seasons. Erosion may be severe on slopes in this type when litter and overstory are removed. Several stands were identified as former *Pinus ponderosa*-*Juniperus deppeana*, or *Pinus ponderosa*-*Quercus gambelii* fire disclimaxes, where *Abies concolor* increased after intensive fire control measures began.

Pseudotsuga menziesii Series

Pseudotsuga menziesii/Bromus ciliatus habitat type (PSME/BRCI; Douglas-fir/fringed brome)

Vegetation.—*Pseudotsuga menziesii* is the dominant timber species in all age classes (fig. 11). *Pinus strobiformis* and *P. ponderosa* are minor components, and *Abies concolor* is absent.

Acer glabrum was present in the two plots sampled. Coverage values ranged from 5% to 10%. *Holodiscus dumosus* was common but had low coverage values. The shrub layer was minor in comparison with graminoids, which covered the entire surface of the plots. *Bromus ciliatus* was a constant graminoid in this habitat type; *Carex foena*, *C. rossii*, and *Trisetum montanum* were abundant. The forb layer also was well represented, at times covering more than 50% of a plot. *Campanula rotundifolia*, *Clematis pseudoalpina*, *Fragaria americana*, *Lathyrus leucanthus*, *Ligusticum porteri*, *Pseudocymopterus montanus*, *Thalictrum fendleri*, and *Valeriana capitata* were abundant. Total cover for undergrowth species often exceeded 100% in stands of this habitat type.

Physical setting.—This habitat type was found at Mount Taylor and the Manzano Mountains, isolated in upper reaches of canyons and on wet ridges. Pockets of deep snow or ground seepage may account for the abundant vegetation. Sites were on north aspects between 9,000 and 9,500 feet (2,745 and 2,895 m). Some slopes were steeper than 50%.



Figure 10.—*Abies concolor*/*Quercus gambelii* habitat type: Pino Canyon, west slope Sandia Escarpment (8,160 feet or 2,490 m). *Abies concolor* and *Pseudotsuga menziesii* are codominant, with *Pinus ponderosa* subordinate. *Quercus gambelii* is the dominant shrub, often reaching tree size. Grasses and forbs are diverse, but their cover values are low.

Ecotones and adjacent habitats.—The PSME/BRCI HT lies above the ABCO/ACGL HT which is found on moist, cool drainages. Upslope, the ABCO/QUGA HT was commonly found.

Discussion.—The PSME/BRCI HT is a high elevation, cool moist habitat type of the *Pseudotsuga menziesii* series. It was found on sites where environmental conditions restricted the establishment of spruce-fir or mixed conifer forests.

After major disturbances, *Populus tremuloides* is the major successional tree species of this habitat type. *Bromus ciliatus*, *Lathyrus* spp., and *Vicia americana* later increase under the aspen, dominating the undergrowth. Eventually, *Pseudotsuga menziesii* will replace aspen. *Acer glabrum* follows as a late successional species after *Pseudotsuga menziesii* is established.

Fitzhugh et al.⁵ described this habitat type in the Magdalena Ranger District of the Cibola National Forest and in the Mogollon Mountains of the Gila National Forest. Both sample plots in this study had prominent shrub layers in which *Acer glabrum* was dominant; Fitzhugh et al.⁵, however, reported that its presence was variable on the Gila National Forest. This study and the one by Fitzhugh et al.⁵ reported a dense undergrowth in this habitat type which often exceeds 100% coverage.

Sites on which this habitat type was found in this study differed somewhat from those described by Fitzhugh et al.⁵ In this study, plots were located in protected pockets on upper canyon slopes, while in the southern range of the San Mateo Mountains, Fitzhugh et al.⁵ found the habitat type along exposed ridges. The difference may be because both plots in this study were below the 9,600–10,100 feet (2,925–3,080 m) elevational range reported by Fitzhugh et al.⁵ At these lower elevations, the protected pockets may have compensated for the greater amount of snowfall found along higher elevation ridges.



Figure 11.—*Pseudotsuga menziesii*/*Bromus ciliatus* habitat type: Capilla Peak (9,160 feet or 2,790 m). *Pseudotsuga menziesii* is dominant, and *Pinus strobiformis* is scattered through the stand. *Acer glabrum* often is abundant in the shrub layer. *Bromus ciliatus* dominates the grass layer, and the forb component is diverse with high coverage values.



Figure 12.—*Pseudotsuga menziesii*/*Festuca arizonica* habitat type: Capilla Peak (9,020 feet or 2,750 m). *Pseudotsuga menziesii* dominates, with *Pinus ponderosa* successional, but persisting into later seral stages. *Quercus gambelii* often is present in the shrub layer. *Festuca arizonica* is the dominant graminoid, but *Carex rossii* sometimes is abundant.

***Pseudotsuga menziesii*/*Festuca arizonica* habitat type (PSME/FEAR HT; Douglas-fir/Arizona fescue)**

Vegetation.—*Pseudotsuga menziesii* is dominant in all age classes; seedlings and small saplings sometimes exceed 200 stems per acre (494/ha) (fig. 12). Regeneration by other species, however, is poor. *Abies concolor* is absent or accidental except along ecotones, while *Pinus strobiformis* is minor or absent. *Pinus ponderosa* is a major seral species, with mature trees persisting in older stands. *P. ponderosa* increases in abundance near transitions with *P. ponderosa* habitat types. *Populus tremuloides* is the major early successional species at upper elevations on cool, moist sites.

The shrub layer of this habitat type is sparse; total cover is less than 5%. *Quercus gambelii* is the most common species, and *Acer glabrum*, *Berberis repens*, and *Holodiscus dumosus* occasionally are present. The grass stratum is very well developed; total coverage being over 40% in some plots, with an average of 25%. *Festuca arizonica* is the dominant species. Other common graminoids include *Bromus ciliatus*, *Carex rossii*, *Koeleria nitida*, *Muhlenbergia montana*, *Poa fendleriana*, and *Sitanion hystrix*. In contrast to the shrub-dominated *Abies concolor* types, grasses are characteristic of *Pseudotsuga menziesii* habitat types on the Cibola National Forest. There was little diversity and coverage of forbs in this habitat type. Nearly constant species included *Campanula rotundifolia*, *Lathyrus arizonicus*, and *Vicia americana*.

Physical setting.—The PSME/FEAR HT can be found on all aspects, from 8,500 to 9,500 feet (2,590 to 2,895 m). It is less common on north aspects, however, where it may be replaced by the ABCO/QUGA HT. It is found near the crest of steep ridges; some plots have slopes steeper than 50%. All stands, except one from the Manzano mountains, were found on Mount Taylor.

Ecotones and adjacent habitats.—The PSME/FEAR HT borders the *Abies concolor* series, usually the ABCO/

QUGA HT, at upper elevations. This transition is from the grass dominated habitat type, PSME/FEAR, to a shrub-dominated type, ABCO/QUGA. Under mesic conditions, the PSME/FEAR HT adjoins the ABCO/ACGL HT. The PSME/FEAR HT is a common habitat type. It is often found on steep, upper, south-facing slopes of canyons, and occasionally occurs far enough downslope to border cool, moist *Picea pungens* habitat types in lower canyons. Transitions to *Picea pungens* types reflect abrupt environmental changes. Because of the isolated nature of *Pseudotsuga menziesii* stands in the Southwest, no situations were observed where the PSME/FEAR HT bordered other habitat types in the *Pseudotsuga menziesii* series. The lower elevational boundary of this habitat type is adjacent to the PIPO/FEAR HT.

Discussion.—The PSME/FEAR HT is the most extensive habitat type of the *Pseudotsuga menziesii* series on the Cibola National Forest. It is abundant on Mount Taylor in the San Mateo Mountains, but probably occurs in the Zuni Mountains as well. The habitat type has been previously described elsewhere (Moir and Ludwig 1979, Alexander et al. 1984b, DeVilce et al. 1986, Fitzhugh et al.⁵).

The description of the PSME/FEAR HT by Moir and Ludwig (1979) differs slightly from that given here. Stands from this study showed abundant regeneration of *Pseudotsuga menziesii* and represented a lower elevational range for the habitat type. Fitzhugh et al.⁵ also described the PSME/FEAR HT throughout the Gila National Forest and the Magdalena District of the Cibola National Forest. In contrast to their descriptions, the PSME/FEAR HT reported in this study for the northern portion of the Cibola National Forest differed as follows: *Abies concolor* was absent except in ecotones, *Muhlenbergia virescens* was absent, and *Pinus strobiformis* was minor to accidental. Also, unlike the Gila National Forest, plots on the Cibola National Forest were not adjacent to other *Pseudotsuga menziesii* habitats; instead, ecotones with habitat types of other forest series were observed. Alexander et al. (1984b) reported a similar situation for the PSME/FEAR HT in northern Arizona.

Successional sequences are unclear within the PSME/FEAR HT. *Pinus ponderosa* and *Pseudotsuga menziesii* maintain themselves under repeated light fires. If *Pinus ponderosa* is fire resistant at an earlier age, periodicity of fire may be important in influencing stand dominance. *Populus tremuloides* is the major early successional species that dominates wetter sites of this habitat type after disturbance. Within the more common, drier sites, a grassy undergrowth with a sparse overstory canopy develops after disturbance to the canopy.

***Pseudotsuga menziesii*/Muhlenbergia montana habitat type (PSME/MUMO HT; Douglas-fir/mountain muhly)**

Vegetation.—*Pseudotsuga menziesii* is the dominant timber species of the overstory, but *Pinus ponderosa* may be codominant, usually in late successional stands (fig. 13). *Pinus strobiformis* often is abundant, but may be absent from some stands. *Abies concolor*, *Pinus edulis*, and *Juniperus deppeana* are accidental.



Figure 13.—*Pseudotsuga menziesii*/Muhlenbergia montana habitat type: Mt. Sedgwick (8,640 feet or 2,635 m). *Pseudotsuga menziesii* dominates, with *Pinus ponderosa* sometimes codominant. *Pinus strobiformis* is a minor climax tree. *Muhlenbergia montana* is abundant, and the forb layer is variable.

The shrub component varies. No species showed high constancy. *Berberis repens* and *Quercus gambelii* are common, but rarely exceeded 5% cover in the stands sampled. *Muhlenbergia montana* is the most consistent undergrowth species in the habitat type, with between 1% and 5% cover. *Festuca arizonica* and *Muhlenbergia virescens* are notably absent. Other common graminoids include *Carex rossii*, *Koeleria nitida*, *Poa fendleriana*, and *Sitanion hystrix*. Average cover for grasses was 5% in this study; average forb cover was 8%. Common forbs include *Artemisia ludoviciana*, *Lithospermum multiflorum*, *Pseudocymopterus montanus*, *Senecio neomexicanus*, and *Thalictrum fendleri*.

Physical setting.—The PSME/MUMO HT is found on ridges of upper, mid, and lower slopes. It ranges from 8,000 to 9,000 feet (2,440 to 2,745 m) in elevation.

Ecotones and adjacent habitats.—The PSME/MUMO HT has been found adjacent to the *Pinus ponderosa*/Muhlenbergia montana habitat types (PIPO/MUMO HT) and the PIPO/FEAR HT. PSME/MUMO occurs over a broad range of environmental conditions, as indicated by the close association of this type with the two *Pinus ponderosa* habitat types. In general, the PIPO/FEAR HT is found on relatively more moist sites than the PIPO/MUMO HT. As elevation increases, the PSME/MUMO HT is replaced by the ABCO/QUGA HT, reflecting a shift from habitat types dominated by grass to those dominated by shrubs.

Discussion.—The PSME/MUMO HT was found only near Mount Sedgwick toward the eastern edge of the Zuni Mountains. Site quality is moderate to poor for *Pinus ponderosa*, and poor for *Pseudotsuga menziesii*. Other than obvious overstory differences, the PSME/MUMO HT is distinguished from the *Pinus ponderosa* types by the abundance of forbs and the shared dominance of the shrubs and graminoids, indicating a more mesic character.

Sites on which the habitat type grows may support a disclimax *Pinus ponderosa* overstory when subjected to frequent fires. Also, *Pinus strobiformis* occurred on some

sites as a mid- to late-successional species. Disturbances that create openings in the canopy may result in increased coverage of graminoids, primarily *Muhlenbergia montana* and *Poa fendleriana*. More mesic sites supported increased shrub cover, while xeric sites supported more grasses.

The PSME/MUMO HT also has been described for the Gila National Forest by Fitzhugh et al.⁵ Many of the plots sampled by these authors were from the southern portion of the Cibola National Forest, in the San Mateo Mountains.

***Pseudotsuga menziesii*/Quercus gambelii habitat type (PSME/QUGA HT; Douglas-fir/Gambel oak)**

Vegetation.—*Pseudotsuga menziesii* is the dominant timber species (fig. 14). Other conifers usually are absent from older stands. *Pinus ponderosa* can occur in early successional stands, with *Juniperus scopulorum* a subordinate in the lower portion of the canopy. *Quercus gambelii* also will grow to tree form and assume patchy dominance within that part of the canopy.

The shrub layer is dominated by *Quercus gambelii* with coverage values commonly over 20%. *Berberis repens*, *Pachystima myrsinites*, *Ribes cereum*, and *Symphoricarpos oreophilus* are common but less abundant than *Quercus gambelii*. The graminoids are a minor element in this type, and *Bromus ciliatus*, *Carex geophila*, *Poa fendleriana*, and *Sitanion hystrix* are common. Forbs are highly variable; species that favor cooler sites are most common. *Erigeron speciosus*, *Fragaria americana*, *Galium boreale*, *Lathyrus arizonicus*, and *Mertensia franciscana* were abundant but not constant.

Physical setting.—The PSME/QUGA HT was found in canyons at mid-elevations ranging from 7,500 to over 8,500 feet (2,285 to over 2,590 m) and on all aspects. The ground surfaces of sampled plots were rocky and covered with a shallow litter layer. All plots were on heavily fractured limestone parent material. The critical limitation



Figure 14.—*Pseudotsuga menziesii*/Quercus gambelii habitat type: Lookout Mt. (8,580 feet or 2,615 m). *Pseudotsuga menziesii* is often the only tree present. *Pinus ponderosa* is seral. *Quercus gambelii* dominates the shrub layer, and *Berberis repens* is common. *Poa fendleriana* and *Sitanion hystrix* are common grasses.

to the occurrence of this habitat type is the availability of cool canyon sites.

Ecotones and adjacent habitats.—The PSME/QUGA HT was found adjacent to habitat types of the ponderosa pine series, often the PIPO/FEAR HT. The PSME/QUGA HT of the Cibola National Forest is distinct from other *Pseudotsuga menziesii* habitat types, because it occurs in cool canyons which are adjacent to warmer forest types.

Discussion.—Only two plots of the PSME/QUGA HT were found on the Cibola National Forest, and both were in the Zuni Mountains. However, they clearly confirmed the identity of the habitat type described in earlier studies in the Southwest (Alexander et al. 1984a, Alexander et al. 1984b, Fitzhugh et al.⁵). The stands on the Cibola are most likely the typic phase of this habitat type. The sites are located in topographic situations similar to that described for the PSME/QUGA HT in northern Arizona (Alexander et al. 1984b), where it was found along cool drainages of the Mogollon Rim. This habitat type is not restricted to canyon sites in other areas (Alexander 1984a, Fitzhugh et al.⁵).

The site quality of the PSME/QUGA HT for timber production is poor, and stands can be heavily infected with mistletoe. Soils are shallow and likely to be damaged by most management activities.

PONDEROSA PINE HABITAT TYPES

***Pinus ponderosa* Series**

***Pinus ponderosa*/Quercus gambelii habitat type (PIPO/QUGA HT; ponderosa pine/Gambel oak)**

Vegetation.—The timber overstory is dominated by *Pinus ponderosa* (fig. 15). Other timber species are noticeably absent. In mature stands, *Quercus gambelii* in tree form will dominate the lower part of the canopy. Three phases are recognized for this habitat type: *Quercus gambelii* (QUGA) typic phase, *Pinus edulis* (PIED) phase, and the *Schizachyrium scoparium* (Andropogon scoparius) (SCSC) phase. In the *Pinus edulis* phase, *Pinus edulis* and *Juniperus deppeana* are abundant. These two species also are common in the *Schizachyrium scoparium* phase, but are not as constant as they are in the *Pinus edulis* phase. Both are absent from the typic phase.

Quercus gambelii (QUGA) typic phase.—The shrub layer of the typic phase is dominated by *Quercus gambelii*, which exhibits cover values consistently greater than 5% and often more than 25%. *Quercus gambelii* often occurs as patchy clumps throughout the stand. *Berberis repens* shows high constancy with a trace to 5% cover.

There are three consistent graminoid species present in this phase: *Muhlenbergia montana*, *Poa fendleriana*, and *Sitanion hystrix*. These species together maintain 1% to 5% cover, occasionally over 10%, but always less than the cover of *Quercus gambelii*. *Festuca arizonica* and *Muhlenbergia virescens* are absent.

Forbs show little constancy. *Bahia dissecta*, *Lithospermum multiflorum*, and *Senecio neomexicanus* are common, but usually in trace amounts.

Pinus edulis (PIED) phase.—*Quercus gambelii* is the dominant shrub, but cover values, rarely over 20%, tend to be lower than in the typic phase. *Berberis repens* is uncommon and is rarely over 1% cover. Common shrubs include *Cercocarpus montanus*, while *Quercus undulata* and *Yucca* spp. occur under drier conditions.

Poa fendleriana and *Sitanion hystrix* are the most consistent graminoid components, and *Muhlenbergia montana* is absent or minor in cover. *Bouteloua gracilis* is also common, but rarely with more than 1% cover. Total graminoid cover is less than that of shrubs.

Forbs are a minor aspect of the undergrowth, with cover rarely exceeding 1%. *Artemisia ludoviciana*, *Eriogonum racemosum*, *Penstemon* spp., and *Senecio neomexicanus* are common species present.

Schizachyrium scoparium (SCSC) phase.—Shrub species, other than *Quercus gambelii*, are uncommon and exhibit low coverage values. The graminoid component of the SCSC phase is well developed, with total coverage values equal to or often exceeding that of the shrubs. *Schizachyrium scoparium* is diagnostic, with coverage values ranging from 1% to 10%. *Koeleria nitida*, *Muhlenbergia montana*, *Poa fendleriana*, and *Sitanion hystrix* are all common; coverage values are 1% or higher. *Muhlenbergia montana* often has greater than 5% coverage. Total graminoid coverage averaged 15% for the sampled stands. Forbs are minor, with *Lotus wrightii*, *Penstemon* spp., and *Senecio neomexicanus* common.

Physical setting.—The PIPO/QUGA HT can be found in a variety of topographic situations—canyons, ridges, and mesas. The typic phase occurs between 7,500 and 8,500 feet (2,285 and 2,590 m), on all aspects. Soil is sometimes exposed on the site, usually where an oak canopy is lacking. However, litter cover normally averages 92%. The PIED phase is more consistently found at lower elevations than the typic phase—between 7,200 and 8,200 feet (2,195 and 2,500 m). It is in canyon bottoms at the lower end of this elevational range. Rock cover increases in the PIED phase, ranging from 5% to over 25%, with litter coverage averaging 87% for the measured plots. The SCSC phase occurs between 7,400 and 8,500 feet (2,255

and 2,590 m) and occupies sites on rocky ridges. Rock cover averages 35% over a range of 17–60%. Litter cover is reduced to an average of 61%.

Ecotones and adjacent habitats.—The PIPO/QUGA HT is adjacent to other habitat types of the *Pinus ponderosa* series, often the PIPO/FEAR HT. At lower elevations, the PIED phase of the habitat type usually is found next to pinyon-juniper woodlands. At higher elevations, the PIPO/QUGA HT adjoins the ABCO/QUGA HT where transitions to more mesic conditions are abrupt.

Discussion.—The PIPO/QUGA HT is common throughout the Cibola National Forest, where the most extensive stands are in the Zuni Mountains near Oso Ridge. The PIED phase is prevalent in canyons on the west escarpment of the Sandia Crest and in the Manzano Mountains.

This habitat type represents a shrub dominated *Pinus ponderosa* habitat type, as distinguished from grass types such as the PIPO/FEAR HT. Although the SCSC phase of the habitat type has a well-developed graminoid component, it also has a prominent shrub layer.

The PIPO/QUGA HT discussed here has been described by others (Alexander et al. 1984a, DeVilce et al. 1986, Fitzhugh et al.⁵), reflecting its widespread occurrence throughout southwestern forests. Many PIPO/POFE communities identified by Hanks et al. (1983) are really PIPO/QUGA HTs according to Fitzhugh et al.⁵ The type occurs in northern Arizona, but it is more common in New Mexico forests.

Although the habitat type occurs throughout the Southwest, the various phases are distinctly associated with specific National Forests. For example, both the typic and the *Pinus edulis* phases were identified on the Cibola National Forest, as well as the Carson and Santa Fe National Forests in northern New Mexico by DeVilce et al. (1986). In contrast, the *Festuca arizonica* phase was found in northern New Mexico but not on the Cibola National Forest. Similarly, Fitzhugh et al.⁵ identified the *Muhlenbergia longiligula* phase on the Gila National Forest, but it was not found on the Cibola National Forest.

The SCSC phase of the PIPO/QUGA HT is defined here for the first time in the Southwest; it represents a rocky environment of the habitat type. The PIPO/QUGA HT tended to occur on rocky and harsh sites in the Cibola National Forest, which is similar to its occurrence in northern Arizona (Hanks et al. 1983).

***Pinus ponderosa*/Festuca arizonica habitat type (PIPO/FEAR HT; ponderosa pine/Arizona fescue)**

Vegetation.—*Pinus ponderosa* is the dominant timber species (fig. 16). Regeneration can be heavy—over 300 stems per acre (740/ha). *Pinus edulis* often is abundant in size classes less than 2 inches (5.1 cm) d.b.h., but it is not consistently present. *Juniperus deppeana* is common; however, it usually occurs along the ecotone with pinyon-juniper woodland.

Quercus gambelii can dominate the shrub layer, although total shrub cover is less than that of grasses. Graminoids dominate the undergrowth, and *Festuca*



Figure 15.—*Pinus ponderosa*/*Quercus gambelii* habitat type: Sinking Spring Canyon (8,230 feet or 2,510 m). *Pinus ponderosa* dominates the canopy. *Quercus gambelii* is the dominant shrub in a low canopy.

arizonica is the dominant species. Forbs are a minor element of the undergrowth.

***Festuca arizonica* (FEAR) typic phase.**—*Festuca arizonica* dominates the undergrowth with an average cover of 13%. *Muhlenbergia montana* and *Poa fendleriana* are common and can dominate sites following disturbance. Other common grasses and sedges include *Carex rossii*, *Koeleria nitida*, and *Sitanion hystrix*. Shrubs which can be common are *Ceanothus fendleri*, *Quercus gambelii*, and species of *Ribes*. However, shrubs rarely have more than trace coverage. Forb cover averaged 8% on the plots. Common species include *Antennaria parviflora*, *Erigeron flagellaris*, *Lotus wrightii*, and *Senecio neomexicanus*.

***Bouteloua gracilis* (BOGR) phase.**—*Pinus edulis* often dominates the reproduction stage, and may become codominant with *Pinus ponderosa*. *Juniperus deppeana* is a minor species. The undergrowth is dominated by *Festuca arizonica*; *Bouteloua gracilis* is consistent with coverage values varying from a trace to 2%. The shrub layer is minimal and *Quercus gambelii* is often absent. *Yucca angustissima*, *Y. baccata*, and *Y. schottii* are found within this phase. Forbs include *Antennaria parviflora*, *Erigeron flagellaris*, and *Senecio neomexicanus*.

***Quercus gambelii* (QUGA) phase.**—*Abies concolor* and *Pseudotsuga menziesii* are accidental trees along ecotones with mixed conifer forests. The undergrowth is dominated by grasses, *Festuca arizonica* being the most abundant. *Muhlenbergia montana*, *Poa fendleriana*, and *Sitanion hystrix* also are common. The shrub layer differs from that of other phases in that *Quercus gambelii* in tree form becomes a part of the lower overstory canopy. Other shrub species are rare or occur only in trace amounts.

Physical setting.—The typic phase is found on lower to upper slopes of ridges at elevations from 7,900 to 9,500 feet (2,410 to 2,895 m). All aspects are represented and slopes vary from slight to steep (over 40%). The mean cover for exposed rock was 15%, for litter 81%. The



Figure 16.—*Pinus ponderosa*/*Festuca arizonica* habitat type: Cottonwood Creek (8,120 feet or 2,475 m). *Pinus ponderosa* is dominant; other large conifers are absent or accidental. The shrub layer is noticeably reduced; *Ribes* species and *Quercus gambelii* sometimes are present. *Festuca arizonica* is abundant, and *Carex rossii* common. Forbs are abundant, with *Achillea millifolium* and *Pseudotsugomyrtes montanus* often common.

QUGA phase ranges from 7,500 to 9,500 feet (2,285 to 2,895 m) on ridges, and occurs on all aspects and on moderate slopes. The BOGR phase is found between 7,300 and 8,500 feet (2,225 and 2,590 m) in elevation and on all aspects of moderate (30%) to steep (56%) slopes. Bare rock cover, mostly composed of fractured basalt, sometimes approached 50%.

Ecotones and adjacent habitats.—At high elevations, the typic phase of the PIPO/FEAR HT is adjacent to habitat types characteristic of mixed conifer forests: PSME/MUMO HT, PSME/FEAR HT, or the ABCO/QUGA HT. Lower elevations support ecotones with a variety of *Pinus ponderosa* habitat types and pinyon-juniper woodlands. On mesas near Mount Taylor, the typic phase of the PIPO/FEAR HT can be found in isolated patches on volcanic hills surrounded by pinyon-juniper woodlands. The QUGA phase is adjacent to the typic phase in transitional areas with the mixed conifer forest. Hanks et al. (1983) noted that the QUGA phase can be found on rocky outcroppings in northern Arizona. The BOGR phase is found near pinyon-juniper woodlands and may exist as isolated pockets within woodlands where *Pinus ponderosa* becomes established.

Discussion.—Because of abundant grasses, the FEAR phase of this habitat type is commonly grazed. Heavy grazing may cause a shift in abundance to *Muhlenbergia montana*, *Poa fendleriana*, and *Sitanion hystrix*, depending on the season and intensity of grazing. The sites are highly productive for timber as well.

Although few plots were sampled ($N = 2$), enough information was provided to validate the presence of the BOGR phase by comparing the limited data with that of other studies where sampling was more intense (Hanks et al. 1983, DeVelice et al. 1986, Fitzhugh et al.⁵). The prominent graminoid cover in the BOGR phase of the PIPO/FEAR HT promotes use by livestock. Competition between *Pinus edulis* and *Pinus ponderosa* may occur and result in lower productivity for *P. ponderosa*. Hanks et al. (1983) and Fitzhugh et al.⁵ describe further the response of this habitat type to grazing.

Similarly, the occurrence of the QUGA phase was validated by comparison with studies by Hanks et al. (1983) and Fitzhugh et al.⁵ The QUGA phase of the PIPO/FEAR HT is susceptible to oak competition after disturbance. Crown fires or heavy overstory removal may result in the establishment of oak brush thickets and hinder conifer reestablishment. The grass undergrowth will respond to early-season grazing pressure by a shift in composition from the dominant *Festuca arizonica* to increasing amounts of *Muhlenbergia montana* and *Poa fendleriana*. This phase is important for wildlife because of greater stand diversity, food production, and high cover densities.

***Pinus ponderosa*/*Muhlenbergia virescens* habitat type (PIPO/MUVI HT; ponderosa pine/screwleaf muhly)**

Vegetation.—*Pinus ponderosa* is the dominant timber species, with individuals widely scattered (fig. 17). Regenerating trees are few, often less than or equal to the

number of mature stems. *Pinus edulis* is present in smaller size classes and often equals the number of *Pinus ponderosa* stems. *Juniperus deppeana* may be present, particularly on the higher elevation sites. Mean basal area for the sample was 65 square feet per acre (14.9 m²/ha).

The shrub layer varies, but *Quercus undulata* and *Ceanothus fendleri* are common. Total shrub cover rarely exceeds 5%. Graminoid species dominate sites of this habitat type. *Muhlenbergia virescens* is diagnostic, with coverage values over 10%, often appearing in patchy clumps within the stand. *Bouteloua gracilis*, *Carex* spp., *Poa fendleriana*, *Schizachyrium scoparium*, and *Sitanion hystrix* are all common, but coverage value for each rarely exceeds 1%. Total grass cover averaged 19% for the sampled plots. *Festuca arizonica* is absent. Forbs are sparse and usually account for less than 1% of the stand cover. Common species are *Hieracium fendleri*, *Lotus wrightii*, *Senecio neomexicanus*, and *Sisymbrium* spp.

Physical setting.—This type is found on lower to upper slopes of ridges from 7,500 to 8,500 feet (2,285 to 2,590 m). It occurs on all aspects and on shallow to steep slopes. Exposed soil and rock are prevalent on the ground surface in these stands. Litter is most common around grass patches.

Ecotones and adjacent habitats.—Comparison of PIPO/MUVI HT stands on the Cibola National Forest with those from other areas (Hanks et al. 1983, Fitzhugh et al.⁵) suggest that the environment is drier here than elsewhere. Adjacent habitats include pinyon-juniper woodlands at lower elevations. Other ponderosa pine types, commonly the PIPO/QUGA HT and *Pinus ponderosa*/*Muhlenbergia virescens*-*Festuca arizonica* habitat type, are adjacent to the PIPO/MUVI HT at the upper end of the habitat type range. Hanks et al. (1983) and Fitzhugh et al.⁵ also found this type next to mixed conifer forests.

Discussion.—Stands of this habitat type were found in the eastern Zuni Mountains near Bonita Canyon. One stand, near McGaffey Lookout, represented the higher



Figure 17.—*Pinus ponderosa*/*Muhlenbergia virescens* habitat type: McGaffey Lookout (8,160 feet or 2,490 m). *Pinus ponderosa* dominates, with *Juniperus deppeana* and *Pinus edulis* subordinate. *Quercus gambelii* sometimes is present, but the shrub layer usually is minor. *Muhlenbergia virescens* is the dominant grass, while the forb layer is minor.



Figure 18.—*Pinus ponderosa*/*Muhlenbergia virescens*-*Festuca arizonica* habitat type: Little Water Canyon (8,320 feet or 2,535 m). *Pinus ponderosa* is the dominant overstory species, with other species accidental or rare. *Quercus gambelii* and *Berberis repens* are common in the shrub layer. *Festuca arizonica* and *Muhlenbergia virescens* are the common grass species, their codominance being diagnostic for this type. Forb constancy is variable.

elevational range of the type. On the Cibola National Forest, the type has been identified as the typic phase described in other studies (Hanks et al. 1983, Fitzhugh et al.⁵).

The PIPO/MUVI HT of the Cibola National Forest is a sparsely timbered type on cobbly soils. Both the study by Hanks et al. (1983) and that of Fitzhugh et al.⁵ showed a higher number of small *Pinus ponderosa* trees and denser timber stands than the present study.

The PIPO/MUVI HT is grass dominated and exhibits xeric features of the moisture gradient where *Pinus ponderosa* dominates. Fitzhugh et al.⁵ found that site conditions for this habitat type were drier in southern New Mexico than in Arizona. In contrast, Hanks et al. (1983) identified the PIPO/MUVI HT as the most mesic ponderosa pine type in northern Arizona. Stands on the Cibola National Forest illustrate the driest range of the PIPO/MUVI HT, being found adjacent to pinyon-juniper woodlands. This variation in ecological position may represent a consistent geographical shift from southwest to northeast New Mexico and from west to east throughout its range.

Successional trends in stands of the PIPO/MUVI HT were not clear. It is possible that *Pinus edulis* may increase with fire exclusion, but *Pinus ponderosa* would still be present. Fuel levels are low, reducing fire intensities and creating patchy burns. Grazing likely would lead to a decrease in *Muhlenbergia virescens* and an increase in *Bouteloua gracilis* and *Poa fendleriana*, particularly with early season grazing.

***Pinus ponderosa*/*Muhlenbergia virescens*-*Festuca arizonica* habitat type (PIPO/MUVI-*FEAR* HT; ponderosa pine/screwleaf muhly-Arizona fescue)**

Vegetation.—*Pinus ponderosa* is the dominant timber species. All other conifer species are accidental or rare (fig. 18). *Quercus gambelii* is the dominant tall shrub, and *Berberis repens* also is common.

Graminoids dominate the undergrowth of this habitat type; both *Festuca arizonica* and *Muhlenbergia virescens* are abundant. Their codominance is diagnostic for this type. Other common species include *Carex rossii*, *Koeleria nitida*, *Poa fendleriana*, and *Sitanion hystrix*.

Forb cover is more diverse compared to other grass-dominated ponderosa pine habitat types. Species may include *Hieraceum fendleri*, *Lithospermum multiflorum*, *Lotus wrightii*, *Penstemon* spp., and *Senecio neomexicanus*.

Physical setting.—This habitat type, based on a larger sample, has been described for northern Arizona (Hanks et al. 1983) and for the Gila National Forest⁵. In both studies, it was found between 8,000 and 8,700 feet (2,440 and 2,650 m) in elevation. It occurs on all aspects of varying slope.

Ecotones and adjacent habitats.—The one sample of this habitat type was found on a north-facing slope with *Picea pungens* stands in a nearby canyon, a typical location according to Fitzhugh et al.⁵ The PIPO/FEAR HT and the PIPO/MUVI HT are common adjacent habitat types.

Discussion.—The PIPO/MUVI-FEAR HT is not common on the Cibola National Forest and is represented by only one plot in this study. However, this was clearly a PIPO/MUVI-FEAR HT according to descriptions from other areas where the type is more common (Hanks et al. 1983, Fitzhugh et al.⁵). The one area sampled may be descriptive of the QUGA phase of the habitat type identified by Hanks et al. (1983), but data are inconclusive and it is retained in the typic phase.

***Pinus ponderosa*/Muhlenbergia montana habitat type (PIPO/MUMO HT; ponderosa pine/mountain muhly)**

Vegetation.—*Pinus ponderosa* is the dominant overstory species (fig. 19). *Pinus edulis* and *Juniperus deppeana* are present in the younger age classes, where they are nearly as abundant as *Pinus ponderosa*. Other conifer tree species are absent, but *Quercus gambelii* in tree form can be a minor component of the overstory.

Total shrub cover, which is dominated by the shrubby form of *Quercus gambelii*, rarely exceeds 5% in this habitat type. Other shrubs which may be present are *Berberis repens*, *Ceanothus fendleri*, and *Yucca baccata*.

Graminoids are the dominant undergrowth species and often exceed 15% cover. *Muhlenbergia montana* is constant and is dominant or codominant with other graminoids. Other common species include *Carex rossii*, *Koeleria nitida*, *Poa fendleriana*, and *Sitanion hystrix*.

Forbs are minor in this habitat type; common species include *Lotus wrightii*, *Penstemon* spp., and *Senecio neomexicanus*.

Physical setting.—The PIPO/MUMO HT is common on west-, south-, and east-facing slopes, and occasionally is found on north aspects. It occurs on lower to upper slopes of ridges between 7,500 and 8,500 feet (2,285 and 2,590 m). Exposure of bare rock and soil is common on these sites, each averaging about 10%.

Ecotones and adjacent habitats.—The PIPO/MUMO HT is often adjacent to the PIPO/FEAR HT. The transi-



Figure 19.—*Pinus ponderosa*/Muhlenbergia montana habitat type: Stinking Springs Canyon (8,150 feet or 2,485 m). *Pinus ponderosa* dominates the canopy. Shrub cover is low, with *Muhlenbergia montana* and *Poa fendleriana* dominating the grass cover.

tion is marked by the appearance of *Festuca arizonica*. Occasionally the PIPO/QUGA HT will be adjacent. At lower elevations, the transition may be directly to pinyon-juniper woodlands. Higher elevations often support the PSME/MUMO HT, where there is an increase in forb diversity.

Discussion.—The PIPO/MUMO HT is widespread in the Zuni Mountains and the Mount Taylor region. One stand of this habitat type was found in the Manzano Mountains, but others probably occur in the Sandia Mountains as well.

Grazing is widespread, and where pressure is intense, *Poa fendleriana* may increase in cover.

This habitat type occurs in northern New Mexico (DeVelice et al. 1986) and in the Gila National Forest⁵. It was not found in northern Arizona, but according to Fitzhugh et al.,⁵ it may be represented by some plots in the PIPO/POFE community type described by Hanks et al. (1983).

***Pinus ponderosa*/Bouteloua gracilis habitat type (PIPO/BOGR HT; ponderosa pine/blue grama)**

Vegetation.—*Pinus ponderosa* is the dominant timber species in all size classes (fig. 20). *Pinus edulis* is present, but usually as scattered individuals in the younger age classes. *Juniperus deppeana* is common, but not as consistent as *Pinus edulis*. *Quercus gambelii* can occur in tree form. *Juniperus deppeana*, *Pinus edulis*, and *Q. gambelii* are minor climax species.

Quercus gambelii is the only shrub that consistently occurs on these sites. Cover values may reach 10%.

Graminoids dominate the undergrowth of this habitat type. *Bouteloua gracilis* is constant and dominates mature sites. Cover values range from 5% to over 30%. *Koeleria nitida*, *Muhlenbergia montana*, *Poa fendleriana*, and *Sitanion hystrix* are common and abundant. Species of *Stipa* occasionally are present. Average grass cover for the sample plots was over 30%.

Forbs are minor in occurrence. Common species include *Artemisia ludoviciana*, *Erigeron flagellaris*, *Lotus wrightii*, *Penstemon* spp., and *Senecio neomexicanus*.

Physical setting.—The PIPO/BOGR HT can be found throughout the Cibola National Forest in isolated stands on ridges. It may be found on all aspects at elevations ranging from 7,500 to 8,500 feet (2,285 to 2,590 m). In the upper elevation range of the habitat type, it occurs on warmer aspects—west and southwest.

Ecotones and adjacent habitats.—At higher elevations, the type may be adjacent to an ABCO series habitat type, commonly the ABCO/QUGA HT. Within ponderosa pine forests, the PIPO/BOGR HT often forms mosaics with the PIPO/MUMO HT or occasionally occurs as patches within the PIPO/QUGA HT.

Discussion.—The PIPO/BOGR HT was previously described by Hanks et al. (1983), DeVelice et al. (1986), and Fitzhugh et al.⁵ Factors leading to the creation of a suitable environment for the PIPO/BOGR HT are not clear. At higher elevations, its occurrence alongside the *Abies concolor* series may be an expression of warmer aspects. Also, soils and drainage may explain the shift from shrub-dominated stands—PIPO/QUGA HT or ABCO/QUGA HT—to the grass-dominated PIPO/BOGR HT.

Because of the heavy grass cover in this type, it may be subjected to intense grazing, which tends to increase the density of *Bouteloua gracilis*, *Poa fendleriana*, and many forb species. Overgrazing may decrease grass cover, expose more soil, and increase disturbance indicator species such as *Artemisia* spp. and *Hymenoxys* spp.

The PIPO/BOGR HT appears to be common in southwestern forests according to Hanks et al. (1983), DeVelice et al. (1986), and Fitzhugh et al.⁵ The PIPO/BOGR HT on the Cibola National Forest may be identical to the *Quercus gambelii* phase described by the above authors. However, the plots in this study were not as xeric as those described elsewhere and data were inadequate. Hence, it was identified as the typic phase.



Figure 20.—*Pinus ponderosa*/*Bouteloua gracilis* habitat type: west slope Sandia Escarpment (8,220 feet or 2,505 m). *Pinus ponderosa* is dominant but sparse. *Quercus gambelii* sometimes has relatively high coverage values in the shrub layer. *Bouteloua gracilis* dominates the grass layer.

***Pinus ponderosa*/Cinder soils habitat type (PIPO/Cinder HT; ponderosa pine/cinder soils)**

Vegetation.—*Pinus ponderosa*, the major timber species, is represented by scattered mature individuals and few trees in the regeneration class (fig. 21). *Pinus edulis* is present, but with fewer individuals than *P. ponderosa*. *Juniperus scopulorum* may be present, but it is not abundant. The average basal area measured was 45 square feet per acre (10.3 m²/ha).

Although *Ribes cereum* frequently is present in stands represented by the PIPO/Cinder HT, it was not found in sampled plots of this study. Other shrubs occasionally include *Holodiscus dumosus* and *Quercus gambelii*. The undergrowth is dominated by graminoids, which appear in patchy clumps throughout the stand. *Muhlenbergia montana* is prominent and has coverage values over 10%. Other consistent species include *Poa fendleriana*, *Schizachyrium scoparium*, and *Sitanion hystrix*. *Bouteloua gracilis*, *Carex rossii*, and *Koeleria nitida* are less consistent, but common. Forbs are diverse but account for less than 5% cover; *Bahia dissecta*, *Cryptantha jamesii*, *Ipomopsis aggregata*, *Lithospermum multiflorum*, *Lotus wrightii*, *Lupinus* spp., and *Penstemon barbatus* are common.

Physical setting.—The diagnostic feature of this habitat type is the basaltic cinder soil, which is characteristically porous in the upper horizon and is subject to slippage on steeper slopes. The droughty nature of these easily drained and unstable soils results in stands with open canopies and patchy grass cover. Sites occupied by the habitat type occur on all aspects from 7,700 to 8,500 feet (2,345 to 2,590 m).

Ecotones and adjacent habitats.—The PIPO/Cinder HT is an isolated habitat type. It is found only in the southeast Zuni Mountains in the cinder hills near Cerro Bandera and Twin Craters. The pinyon-juniper woodland occurs along the lower elevations of these cinder hills.

Discussion.—The PIPO/Cinder HT, although poorly rated for timber production, covers a large area in the Zuni Mountains. It is similar in vegetation composition to the PIPO/MUMO HT, but differs in overstory abundance, prominent soils, and diversity of forbs. Although only four plots were measured for this habitat type, the consistency of the data warrants a separate habitat type classification.

Soils of this habitat type are unstable and shift easily following disturbance. Successional relationships are unclear. However, shrub species such as *Fallugia paradoxa* and *Ribes cereum* may increase after disturbance to sites.

Hanks et al. (1983) found a ponderosa pine habitat type on cinder soils in northern Arizona, the *Pinus ponderosa*/*Bouteloua gracilis* habitat type *Andropogon hallii* phase, which showed a close affinity to other dry ponderosa pine types. The habitat type found in the Cibola National Forest differs from the phase in northern Arizona and from other *Pinus ponderosa* types. To emphasize its unusual characteristics, it is best described as a separate habitat type. More intensive sampling of cinder hill sites in the future may result in their reclassification into

geographically disjunct phases of one or more related habitat types.

Other Ponderosa Pine Habitat Types

Two additional habitat types were found on the Cibola National Forest, but data were inadequate to provide full type descriptions because of their limited nature. They were, however, distinctive enough to warrant recognition for further assessment and research.

The one sample plot of the *Pinus ponderosa*/Riparian habitat type (PIPO/Riparian HT) was found in the Zuni Mountains, near Sawyer Creek, at 8,290 feet (2,525 m) in elevation (fig. 22). It was located in a cool, moist drainage representative of the mesic portion of the ponderosa pine moisture gradient, but at the lower end of the elevation range of the species. The diagnostic feature of the habitat type appears to be species diversity. *Pinus ponderosa* is the dominant overstory species, and *Quercus gambelii* is the dominant shrub. Twenty-two species of forbs were identified on the one plot and included *Allium* spp., *Galium boreale*, *Iris missouriensis*, *Pseudostellaria jamesiana*, *Thalictrum fendleri*, and *Thermopsis pinetorum*. Graminoids also were diverse; 15 species were found. *Agropyron* spp., *Festuca arizonica*, *Juncus* spp., *Lycurus pheloides*, *Muhlenbergia longiligula*, *M. montana*, and *Poa pratensis* were abundant. Undergrowth cover for the site totaled over 40%.

The *Pinus ponderosa*/Rockland habitat type (PIPO/Rockland HT) previously described by Fitzhugh et al.⁵ also was found in the Zuni Mountains on the southwestern slope of Oso Ridge at 8,100 feet (2,470 m) (fig. 23). This habitat type is characterized by very little soil or litter and represents the dry end of the moisture gradient. The small amount of vegetation is sparse and grows in pockets of accumulated soil in cracks and depressions of exposed bedrock. These conditions may suggest early successional responses to disturbance, but the age of the



Figure 21.—*Pinus ponderosa*/Cinder soils habitat type: Cinder Hills, Zuni Mountains (7,940 feet or 2,420 m). *Pinus ponderosa* is the dominant overstory species, with scattered *Pinus edulis*. The shrub layer is minimal, but *Holodiscus dumosus* and *Ribes* species can be found. *Muhlenbergia montana* and *Poa fendleriana* are the dominant grasses, while forbs are scattered and of minor coverage.



Figure 22.—*Pinus ponderosa*/Riparian habitat type: Sawyer Creek (8,290 feet or 2,525 m). *Pinus ponderosa* is the dominant overstory species, with *Quercus gambelii* the dominant shrub. Forb diversity is high, but no species is indicative of the type. Common grasses may include *Festuca arizonica* and *Muhlenbergia montana*.



Figure 23.—*Pinus ponderosa*/Rockland habitat type: Little Water Canyon (8,100 feet or 2,470 m). *Pinus ponderosa* dominates, and *Juniperus deppeana* is scattered. Forbs and grasses are diverse, but with low coverage values. Bare rock dominates plot surfaces.

overstory (200+ years) indicates the relative stability of the stands. Technically, such stands can be considered an edaphic climax. Mature *Pinus ponderosa* forms a sparse and open canopy. Although coverage by undergrowth species is low, diversity is fairly high. The plot contained 17 forb and 10 graminoid species. *Quercus gambelii* was present in trace amounts. Graminoids included *Aristida arizonica*, *Blepharoneuron tricholepis*, *Bouteloua gracilis*, *Muhlenbergia virescens*, and *Poa fendleriana*. Bare rock exposure was over 70% on this plot. Rockland habitat types, although not widespread, probably are more common than indicated by the one plot.

SUMMARY AND CONCLUSIONS

Twenty-one forest habitat types were identified in this study of the northern portion of the Cibola National

Forest; additionally some types were separated into phases. The habitat types represent six forest series: *Abies concolor*, *Abies lasiocarpa*, *Picea engelmannii*, *Picea pungens*, *Pinus ponderosa*, and *Pseudotsuga menziesii*.

The *Picea engelmannii* series is represented by one habitat type, the PIEN/MOSS HT. Its occurrence on the Cibola National Forest is probably limited to the upper slopes of Mount Taylor. Successional forms of this type should be studied further, because drastic shifts in vegetational composition and site modification are suspected after disturbances. The successional role of *Pseudotsuga menziesii* and *Abies concolor* also should be investigated, especially in regard to the establishment of an overstory canopy under which spruce and fir can regenerate.

The *Abies lasiocarpa* series is represented by three habitat types: ABLA/VAMY, ABLA/ACGL, and ABLA/EREX. The undergrowth in the ABLA/VAMY HT and ABLA/ACGL HT is more shrub dominated than that of the ABLA/EREX HT in which forbs abound. The ABLA/EREX HT is found on Mount Taylor and in the Sandia Mountains; the ABLA/VAMY HT was sampled only on Mount Taylor and the ABLA/ACGL HT only in the Sandia Mountains. Both the *Picea engelmannii* and the *Abies lasiocarpa* series are important watershed forests, because a deep snow pack is retained into the warmer spring season.

The *Picea pungens* series is represented by the PIPU/CAFO and the PIPU/COST HT. The basic difference between these two types is shrub dominance in the PIPU/COST HT and graminoid and forb dominance in the PIPU/CAFO HT. Stands of *Picea pungens* habitat types are few and geographically isolated in the Southwest. These blue spruce forests on the Cibola National Forest are relatively inaccessible and are, therefore, not as disturbed as those found elsewhere. They provide forest diversity associated with abrupt environmental changes from warmer forests on adjacent slopes to canyon-bottom forests that are cooler, more moist, and exhibit greater herbaceous production. Such an environmental edge is a critical aspect of wildlife management (Thomas 1979). The *Picea pungens* habitat types also are important for maintaining streamside integrity, and should be studied further for their response to disturbance.

The two habitat types in the *Abies concolor* series, ABCO/ACGL and ABCO/QUGA, illustrate the less diverse characteristics of the series in the Cibola National Forest than are found in other New Mexico forests (Alexander et al. 1984a, DeVelice et al. 1986, Fitzhugh et al.⁵). The series is more common in the Sandia and Manzano Mountains than on Mount Taylor and in the Zuni Mountains. This may be a result of steep topographical situations and subsequent abrupt environmental changes between the pinyon-juniper woodlands and the cool, moist *Abies concolor* forests in the Sandia and Manzano Mountains. Concurrently, the steep topography reduces the extent of intermediate series—*Pseudotsuga menziesii* and *Pinus ponderosa*. Both habitat types of the *Abies concolor* series are shrub dominated, in contrast to habitat types of lower elevation series which support grass dominated undergrowths.

The *Pseudotsuga menziesii* series is most common in the Zuni Mountains. The two major habitat types of this series, the PSME/FEAR and PSME/MUMO, offer productive timber and grazing potentials. Successional forests of these habitat types should be studied regarding their response to prescribed fires. Under frequent but light fires, succession tends to maintain a *Pinus ponderosa* overstory with increased forb and grass cover. The less common PSME/BRCI HT, however, exhibits abundant grass cover in older stands with little disturbance. The PSME/QUGA HT has a limited distribution on the Cibola National Forest, occurring on low elevation, canyon side slopes. When found on cooler north and east aspects, it provides an overall environmental diversity of a cool, moist forest surrounded by warmer *Pinus ponderosa* forests. Timber productivity is low in the PSME/QUGA HT and successional patterns are not well understood.

The *Pinus ponderosa* series is most abundant in the Zuni Mountains and the Mount Taylor region, whereas its areal extent is limited near the Sandia and Manzano Mountains where *Abies concolor* and *Pseudotsuga menziesii* extend to the pinyon-juniper zone. The preponderance of grass-dominated habitat types is exemplified by six grass habitat types and only one shrub habitat type. The grass cover of the PIPO/QUGA HT increases at its lower elevation ranges. On many sites, competition between oak brush and timber species was apparent, particularly in younger successional stands that originated from intense fires. The grass-dominated habitat types provide grazing, which—with proper intensity and season of use—will maintain desired communities. Overgrazing results in shifts to less palatable species and eventual dominance by invader species. The ponderosa pine forest offers a wide range of sites for potential timber production. Higher growth rates will be found in the PIPO/FEAR HT; lower rates will prevail in the cinder and rock-land habitat types of the Zuni Mountains.

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APPENDIXES

Appendix A. Keys to the Climax Forest Series and Habitat Types of the Northern Portion of the Cibola National Forest

The first step in using keys in habitat type classification is to determine the series level of a particular stand by identifying climax overstory tree species. A climax species is well represented in the overstory of older stands that are in equilibrium with the environment, and also is reproducing in the understory. In contrast, the climax species in younger stands may be reproducing under a canopy even though mature individuals of the species are not present in the overstory. Field investigators must judge whether such reproduction will grow to maturity to become the climax dominant, replacing the existing overstory of seral species. This determina-

tion is especially difficult in mixed conifer forests where any of several associated species, other than the climax tree species, may dominate the overstory.

Furthermore, diagnostic species may not always be present in a particular seral stand because of disturbance or the lack of a seed source. The investigator must compare the stand with the habitat type descriptions in order to correctly identify the habitat type. When choices in the keys are not clear because of stand conditions, descriptions and tables should be used to distinguish between types.

A1. Key to Climax Forest Series

1. PIEN or ABLA present in overstory; regeneration sufficient to confirm their status as climax dominants; PIPU rare, usually absent. PIEN and ABLA series. ----- Key A2
1. PIEN and ABLA absent or accidental, or if present, then PIPU also prominent. ----- 2
2. PIPU present in overstory and/or as reproduction. ----- Key A3
- PIPU series. ----- Key A3
2. PIPU absent; ABCO, PSME, or PIPO present. ----- 3
3. ABCO present in overstory, or prominent in understory; not accidental. Other species present but not as climax dominants. ABCO series. ----- Key A3
3. ABCO absent or accidental, not a dominant component of overstory or understory. ----- 5
5. PSME clearly the dominant climax species; PIPO late successional; ABCO absent or accidental. PSME series. --- Key A4
5. PSME not a strong component of either overstory or understory. PIPO the climax dominant. PIPO series. ----- Key A5

A2. Key to *Picea engelmannii* and *Abies lasiocarpa* Series Habitat Types

1. Undergrowth nearly absent; litter layer thick; moss often abundant; PIEN the dominant overstory species; ABLA a minor overstory component. ----- PIEN/MOSS HT
1. Undergrowth abundant; ABLA a prominent component of the climax stand. ----- 2
2. Forbs dominate the undergrowth; *Erigeron eximius* present, sometimes the major forb. ----- ABLA/EREX HT
2. Shrubs usually dominate the undergrowth; *Bromus ciliatus* the dominant grass; *Erigeron eximius* sometimes present, but always subordinate to the shrubs. ----- 3
3. *Acer glabrum* the prominent shrub, often forming part of the canopy; *Bromus ciliatus* abundant in the undergrowth; *Pseudotsuga menziesii* and *Abies concolor* often present in late successional stands. ----- ABLA/ACGL HT
3. *Acer glabrum* absent; *Vaccinium myrtillus* the abundant shrub in the undergrowth. ----- ABLA/VAMY HT

A3. Key to *Picea pungens* and *Abies concolor* Series Habitat Types.

1. *Picea pungens* abundant in overstory; canyon sites; *Abies concolor* seral or absent. ----- 2
1. *Picea pungens* absent; *Abies concolor* dominant in overstory. ----- 3
2. Graminoids and forbs dominate undergrowth; *Carex foenea* dominant; *Fragaria ovalis* common. ----- PIPU/CAFO HT
2. Shrubs, particularly *Cornus stolonifera*, the dominant feature of undergrowth; sites often found on streamside benches. ----- PIPU/COST HT
3. *Acer glabrum* present, usually the dominant tall shrub; *Quercus gambelii* present, but usually subordinate to *Acer glabrum*. ----- ABCO/ACGL HT
- 3a. *Berberis repens* absent or in trace amounts; *Pseudotsuga menziesii* present, often abundant. ----- ACGL typic phase
- 3b. *Berberis repens* present in greater than trace amounts. ----- BERE phase
- 3c. Sites in cool, wet drainages; coniferous species other than *Abies concolor* absent. ----- RIPARIAN phase
3. *Acer glabrum* absent; *Quercus gambelii* usually the dominant tall shrub. ----- ABCO/QUGA HT

A4. Key to *Pseudotsuga menziesii* Series Habitat Types

1. Shrubs abundant with over 5% cover; *Acer glabrum* or *Quercus gambelii* the dominant species; *Bromus ciliatus* abundant in association with *Acer glabrum*. ----- 2
1. Shrubs may be present, but usually less than 5% cover; if shrubs abundant, then with less cover than either *Festuca arizonica* or *Muhlenbergia montana*. ----- 3
2. *Acer glabrum* an abundant tall shrub; *Bromus ciliatus* often with more than 30% cover; *Quercus gambelii* minor, usually absent. ----- PSME/BRCI HT
2. *Acer glabrum* absent; *Bromus ciliatus* often present but rarely over 5% cover; *Quercus gambelii* the dominant tall shrub. ----- PSME/QUGA HT
3. *Festuca arizonica* the dominant graminoid; *Muhlenbergia montana* usually present, but always in association with *F. arizonica*. ----- PSME/FEAR HT
3. *Festuca arizonica* absent; *Muhlenbergia montana* abundant, usually dominating graminoids; *Poa fendleriana* also abundant, at times dominant. ----- PSME/MUMO HT

A5. Key to *Pinus ponderosa* Series Habitat Types

1. Site characterized by bare rock covering much of surface. Soil less than 4 inches (10 cm) deep. ----- PIPO/ROCKLAND HT
1. Sites not characterized by bare rock and shallow soils over bedrock. ----- 2
 2. Sites of cinder hills, upper soil composed of loose, unstructured cobbly volcanic cinder; *Muhlenbergia montana* usually the prominent graminoid. ----- PIPO/CINDER HT
 2. Soils not composed of cinders on cinder hill sites. ----- 3
3. Shrubs the dominant component of undergrowth; *Quercus gambelii* present with more than 5% cover, or if less than 5% cover, then shrubs dominant over graminoids and forbs. ----- PIPO/QUGA HT
 - 3a. *Pinus edulis* rare, not abundant in canopy; *Schizachyrium scoparium* absent. ----- QUGA typic phase
 - 3b. *Pinus edulis* sometimes abundant, definite component of overstory or abundant as regeneration; *Schizachyrium scoparium* usually absent or present only with trace amounts of cover ----- PIED phase
 - 3c. *Schizachyrium scoparium* present with 1% cover or more. *Pinus edulis* often present. ----- SCSC phase
3. Graminoids dominate undergrowth; *Quercus gambelii* may be abundant, but graminoid cover exceeds that of *Q. gambelii*. -- 4
 4. *Schizachyrium scoparium* a prominent graminoid, having more than 1% cover. *Quercus gambelii* present with more than 5% cover. ----- PIPO/QUGA HT, SCSC phase
 4. Other grasses dominant. *Schizachyrium scoparium* with 1% or less cover. *Quercus gambelii* present or absent. ----- 5
5. *Festuca arizonica* or *Muhlenbergia montana* the dominant graminoid; *Muhlenbergia virescens* absent. ----- 6
5. *Festuca arizonica* absent, or if present, codominant with *Muhlenbergia virescens*. ----- 7
 6. Wet riparian sites with *Festuca arizonica* and *Muhlenbergia montana* sharing dominance. ----- PIPO/Riparian HT
 6. *Festuca arizonica* usually dominant, upland sites. ----- PIPO/FEAR HT
 - 6a. *Quercus gambelii* less than 5% cover; *Bouteloua gracilis* absent. ----- FEAR typic phase
 - 6b. *Quercus gambelii* with more than 5% cover; *Festuca arizonica* with greater cover than *Q. gambelii*. ----- QUGA phase
 - 6c. *Bouteloua gracilis* present in greater than trace amounts; *Quercus gambelii* less than 5% cover. ----- BOGR phase
7. *Muhlenbergia virescens* present, often the dominant graminoid species; *Festuca arizonica* may be present as codominant. -- 8
7. *Muhlenbergia virescens* absent; other graminoids may be abundant. ----- 9
 8. *Festuca arizonica* absent; *Muhlenbergia virescens* dominant graminoid. ----- PIPO/MUVI HT
 8. *Muhlenbergia virescens* codominant with *Festuca arizonica*, both graminoids obviously more abundant than other species. ----- PIPO/MUVI-FEAR HT
9. *Muhlenbergia montana* abundant, usually dominant; *Poa fendleriana* also abundant, sometimes exceeding *M. montana*; *Bouteloua gracilis* rare, usually absent. ----- PIPO/MUMO HT
9. *Bouteloua gracilis* the dominant grass, usually over 5% cover; *Stipa* species may be abundant. ----- PIPO/BOGR HT

Appendix B. Plant Species Identified in Study¹

Trees

Abies concolor
Abies lasiocarpa
Acer negundo
Juniperus deppeana
Juniperus monosperma
Juniperus osteosperma
 (J. *utahensis*)
Juniperus scopulorum
Picea engelmannii
Picea pungens
Pinus edulis
Pinus ponderosa
*Pinus strobiformis*²
Populus tremuloides
Pseudotsuga menziesii
Quercus arizonica
Quercus gambelii
Quercus grisea

Shrubs

Acer glabrum
Alnus oblongifolia
Alnus tenuifolia
Amelanchier utahensis
Berberis repens
 (Mahonia *repens*)
Ceanothus fendleri
Ceanothus integriramus
Cercocarpus montanus
 (C. *betuloides*)
Chrysothamnus spp.
Chrysothamnus depressus
Chrysothamnus nauseosus
Chrysothamnus viscidiflorus
Cornus stolonifera
 (Swida *sericea*)
Fallugia paradoxa
Fendlera rupicola
Garrya wrightii
Gutierrezia sarothrae
 (Xanthocephalum *sarothrae*)
Holodiscus dumosus
Hymenoxys acaulis
Hymenoxys richardsonii
Jamesia americana
Juniperus communis
Lonicera spp.
Lonicera arizonica
Lonicera involucrata
Lonicera utahensis
Lycium spp.
Pachistima myrsinites
Physocarpus monogynus
 (P. *malvaceus*)
Potentilla fruticosa
 (Pentaphylloides *floribunda*)
Prunus virginiana
Purshia tridentata
Quercus undulata
 (Q. *gambelii* × Q. *grisea*)
Rhus trilobata
 (R. *aromatica*)
Ribes spp.
Ribes cereum
Ribes leptanthum
Robinia neomexicana
Rosa spp.
Rosa woodsii
Rubus neomexicanus
Rubus parviflorus

Shrubs continued

Rubus strigosus
 (R. *idaeus*)
Salix spp.
Salix scouleriana
Sambucus neomexicanus
Symphoricarpos oreophilus
Tetradymia canescens
Toxicodendron rydbergii
 (T. (Rhus) *radicans*)
Vaccinium myrtillus
 (V. *oreophilum*)
Vitis arizonica
Yucca angustissima
Yucca baccata
Yucca schottii

Graminoids

Agropyron smithii
Agropyron trachycaulum
Agrostis scabra
Agrostis semiverticillata
Andropogon gerardi
Aristida arizonica
Aristida fendleriana
Blepharoneuron tricholepis
Bouteloua curtipendula
Bouteloua gracilis
Bromus spp.
Bromus carinatus
Bromus ciliatus
 (B. *richardsonii*)
 (Bromopsis *ciliata*)
Bromus frondosus
 (Bromopsis *frondosa*)
Bromus marginatus
 (Ceratochloa *marginata*)
Bromus tectorum
Calamagrostis canadensis
Calamagrostis inexpansa
 (C. *neglecta*)
Carex spp.
Carex aurea
Carex foenea
Carex geophila
Carex media
 (C. *norvegica*)
Carex occidentalis
Carex rossii
Carex scoparia
Carex vallicola
Cyperus spp.
Dactylis glomerata
Danthonia californica
Danthonia intermedia
Danthonia parryi
Deschampsia caespitosa
Elymus glaucus
Elymus triticoides
Festuca arizonica
Festuca octoflora
Festuca sororia
Festuca thurberi
Glyceria striata
Juncus spp.
Juncus balticus
 (J. *arcticus*)
Juncus interior
 (J. *tenuis*)
Juncus saximontanus

Graminoids continued

Koeleria nitida
 (K. *cristata*)
 (K. *macrantha*)
 (K. *pyramidata*)
Lycurus phleoides
Melica porteri
Muhlenbergia spp.
Muhlenbergia emersleyi
Muhlenbergia longiligula
Muhlenbergia montana
Muhlenbergia virescens
Oryzopsis micrantha
Panicum bulbosum
Piptochaetium fimbriatum
Poa compressa
Poa fendleriana
Poa nervosa
 (P. *traceyi*)
 (P. *wheeleri*)
Poa palustris
Poa pratensis
Schizachyrium scoparium
 (Andropogon *scoparius*)
Setaria spp.
Sitanion hystrix
 (S. *longifolium*)
Stipa spp.
Stipa comata
Stipa lettermani
Stipa pringlei
Trisetum montanum
 (T. *spicatum*)

Forbs

Achillea millefolium
 (A. *lanulosa*)
Actaea rubra spp. *arguta*
 (A. *arguta*)
Agastache pallidiflora
Ageratina herbacea
 (Eupatorium *herbaceum*)
Agoseris spp.
Agoseris aurantiaca
Agoseris glauca
Allium spp.
Allium cernuum
Allium geyeri
Androsace occidentalis
Antennaria spp.
Antennaria marginata
 (A. *neglecta*)
Antennaria parvifolia
 (A. *aprica*)
Anthericum torreyi
Apocynum cannabinum
Aquilegia chrysantha
Aquilegia elegantula
Arabis fendleri
Arabis pendulina
Aralia racemosa
Arenaria spp.
Arenaria eastwoodiana
Arenaria fendleri
Arenaria lanuginosa
 (A. *confusa*)
 (A. *saxosa*)
Artemisia spp.
Artemisia campestris
 (A. *pacifica*)
Artemisia carruthii

Forbs continued

Artemisia dracuncululus
 (A. *dracunculoides*)
Artemisia franserioides
Artemisia frigida
Artemisia ludoviciana
Asclepias asperula
 (A. *capricornu*)
Aster spp.
Aster foliaceus
Astragalus spp.
Astragalus amplexoxys
*Astragalus egglestonii*³
 (A. *rusbyi*)
Astragalus humistratus
Astragalus mollisimus
Astragalus recurvus
Bahia dissecta
Besseyia plantaginea
Brickellia californica
Brickellia grandiflora
Calliandra humilis
Calochortus spp.
Calochortus gunnisoni
Campanula rotundifolia
Castilleja spp.
Castilleja austromontana
Castilleja integra
Castilleja linariaefolia
Chaptalia alsophila
Chenopodium aff. album
Cirsium spp.
Cirsium calcareum
 (C. *pulchellum*)
Cirsium grahami
Cirsium parryi
Cirsium wheeleri
Clematis ligusticifolia
Clematis pseudoalpina
 (C. *columbiana*)
Corallorhiza spp.
Corallorhiza maculata
Cryptantha spp.
Cryptantha jamesii
Cystopteris fragilis
Delphinium spp.
Draba spp.
Draba helleriana
Drymaria tenella
Dugaldia hoopesii
 (Helenium *hoopesii*)
Echinocereus spp.
 (Mammillaria spp.)
Epilobium paniculatum
Equisetum spp.
Equisetum arvense
Equisetum hiemale
 (E. *hyemale*)
 (Hippochaete *hyemalis*)
Erigeron spp.
Erigeron eximius
 (E. *superbus*)
Erigeron flagellaris
Erigeron formosissimus
Erigeron speciosus
 (E. *macranthus*)
Erigeron platyphyllus
Eriogonum alatum
Eriogonum jamesii
Eriogonum racemosum
Erysimum capitatum

Forbs continued

Euphorbia spp.
Euphorbia lurida
Fragaria americana
 (F. bracteata)
 (F. vesca)
Fragaria ovalis
 (F. virginiana)
Franseria spp.
Galium spp.
Galium boreale
Galium microphyllum
Galium triflorum
Galium wrightii
Geranium spp.
Geranium caespitosum
 (G. fremontii)
Geranium richardsonii
Gilia spp.
Goodyera oblongifolia
Gutierrezia spp.
Habenaria spp.
 (Limnorchis spp.)
Habenaria sparsiflora
Hackelia floribunda
Haplopappus parryi
 (Oreochrysum parryi)
 (Solidago parryi)
Hedeoma drummondii
Hedeoma oblongifolium
Hedyotis pygmaea
 (Houstonia wrightii)
Helianthella parryi
Helianthella quinquenervis
Helianthus spp.
Heterotheca fulcrata
 (H. villosa)
 (Chrysopsis fulcrata)
 (C. villosa)
Heterotheca grandiflora
Heuchera parvifolia
Hieracium fendleri
Hymenopappus filifolius
 (H. lugens)
Hymenopappus mexicanus
Hymenoxys spp.
Hymenoxys acaulis
Hymenoxys bigelovii
Hymenoxys brandegi
Hymenoxys cooperi
Hymenoxys ivesiana
Ipomoea spp.
Ipomopsis aggregata
 (Gilia aggregata)
Iris missouriensis
Kochia spp.

Forbs continued

Lactuca spp.
Lactuca serriola
 (L. scariola)
Lappula redowskii
Lathyrus arizonicus
Lathyrus graminifolius
Lathyrus leucanthus
 (L. lanzwertii)
Lesquerella fendleri
Leucelene ericoides
 (Aster arenosus)
 (A. hirtifolius)
Ligusticum porteri
Linanthus spp.
 (Linanthastrum spp.)
Lithospermum multiflorum
Lotus spp.
Lotus utahensis
Lotus wrightii
Lupinus spp.
Lupinus argenteus
Lupinus kingii
Malaxis soulei
 (M. macrostachya)
Mammillaria spp.
 (Coryphantha spp. in part)
Melilotus albus
Melilotus officinalis
Mertensia ciliatus
Mertensia franciscana
Mirabilis oxybaphoides
Myosotis scorpiodes
Oenothera spp.
Oenothera rosea
Opuntia spp.
Orobancha ludoviciana
Orobancha multiflora
Orthocarpus purpureo-albus
Osmorhiza chilensis
Osmorhiza depauperata
 (O. obtusa)
Oxalis metcalfei
 (O. alpina)
Oxybaphus linearis
 (Mirabilis linearis)
Oxytropis lambertii
Pedicularis spp.
Pedicularis centranthera
Pedicularis grayi
Pellea atropurpurea
Penstemon spp.
Penstemon barbatus
Penstemon bridgesii
Penstemon eatoni

Forbs continued

Penstemon linarioides
Penstemon strictus
Penstemon virgatus
 (P. putus)
Penstemon whippleanus
Petalostemum spp.
Petalostemum canidum
 (Dalea candida)
 (D. oligophylla)
Phacelia spp.
Phlox spp.
Phlox speciosa
Plantago spp.
Polemonium foliosissimum
Polygala alba
Polygonum sawatchense
Potentilla spp.
Potentilla concinna
Potentilla crinita
Potentilla fruticosa
Potentilla hippiana
Pseudocymopterus montanus
Pseudostellaria jamesiana
 (Stellaria jamesiana)
Psoralea tenuiflora
Pteridium aquilinum
Pyrola spp.
Ramischia secunda
 (Pyrola secunda)
 (Orthilia secunda)
Ranunculus inamoenus
Rudbeckia laciniata
Scrophularia parviflora
Sedum spp.
Senecio spp.
 (Packera spp.)
Senecio actinella
Senecio bigelovii
 (Ligularia bigelovii)
Senecio eremophilus
Senecio hartianus
Senecio neomexicanus
Senecio multilobatus
Senecio sacramentanus
Senecio sanguisorboides
Senecio wootonii
Silene laciniata
Silene scouleri
Sisymbrium spp.
 (Thelypodiopsis spp. in part)
Sisymbrium altissimum
Sisymbrium irio
Sisymbrium linearifolium
 (Thelypodiopsis linearifolia)

Forbs continued

Sisyrinchium demissum
 (S. angustifolium)
Smilacina racemosa
Smilacina stellata
Solidago spp.
Solidago sparsiflora
Solidago wrightii
Sphaeralcea grossulariaefolia
Stellaria spp.
Stellaria longifolia
Stellaria umbellata
Streptanthus spp.
Swertia radiata
 (Fraseria speciosa)
Talinum spp.
Taraxacum spp.
Taraxacum laevigatum
Taraxacum officinale
Thalictrum fendleri
Thelesperma megapotamicum
Thermopsis pinetorum
 (T. divaricarpa)
 (T. rhombifolia)
Thlaspi spp.
Thlaspi arvense
Thlaspi montanum
 (T. alpestre)
 (T. fendleri)
Townsendia exscapa
Tragia stylaris
 (T. ramosa)
Tragopogon dubius
Trifolium spp.
Trifolium rusbyi
Trifolium subcaulescens
Urtica gracilis
Valeriana spp.
Valeriana capitata
 (V. capitata ssp. acutiloba)
 (V. arizonica)
Valeriana edulis
Verbascum thapsus
Verbena macdougalii
Verbena wrightii
Veronica spp.
Vicia spp.
Vicia americana
Vicia pulchella
Viguiera multiflora
 (Heliomeris multiflora)
Viola spp.
Viola canadensis
Zigadenus elegans
 (Anticlea elegans)

¹Taxonomic authorities were Lehr (1978), Lehr and Pinkava (1980, 1982), Martin and Hutchins (1980, 1981), and Weber and Johnston (1979).

²A distinction was not made between *Pinus strobiformis* and *P. flexilis* in this study; both species were listed as *P. strobiformis*.

³*Astragalus egglestonii* and *A. rusbyi* are two distinct species, but the names of each have been misapplied to the other species (USDA 1982a, 1982b).

Appendix C. Successional Status of Major Tree Species Within Habitat Types

C = major climax species S = major seral species a = accidental

c = minor climax species s = minor seral species

HABITAT TYPES	Species										
	ABLA	PIEN	PIPU	POTR	ABCO	PSME	PIST	PIPO	QUGA	PIED	JUDE
PIEN/MOSS HT	c	C	.	S	.	s
ABLA/ACGL HT	C	c	.	S	S	S
ABLA/EREX HT	C	C	.	S	s	s
ABLA/VAMY HT	C	C	.	S	s	s
PIPU/CAFO HT	.	c	C	S	a	C	a	a	.	.	.
PIPU/COST HT	.	.	C	S	.	C
ABCO/ACGL HT											
ACGL typic P	.	.	.	S	C	C	c	c	.	.	.
Riparian P	.	.	.	S	C
BERE P	.	.	.	S	C	C	c	c	.	.	.
ABCO/QUGA HT											
ABCO/QUGA HT	C	S	c	S	C	.	.
PSME/BRCI HT	.	.	.	S	.	C	c	c	.	.	.
PSME/FEAR HT	.	.	.	S	a	C	a	S	.	.	.
PSME/MUMO HT	a	C	s	C	.	a	a
PSME/QUGA HT	C	.	s	C	.	.
PIPO/QUGA HT											
QUGA typic P	C	C	a	a
PIED P	C	C	c	c
SCSC P	C	C	c	c
PIPO/FEAR HT											
FEAR typic P	C	c	c	c
BOGR P	c	.	.	C	a	c
QUGA P	a	a	.	C	C	c	c
PIPO/MUVI HT	C	a	c	c
PIPO/MUVI-FEAR HT	C	c	.	.
PIPO/MUMO HT	c	.	.	C	c	c
PIPO/BOGR HT	C	c	c	c
PIPO/Cinders HT	C	.	c	.
PIPO/Riparian HT	C	c	.	.
PIPO/Rockland HT	C	.	.	.

Species and size class	PIEN/ Moss ² HT (N = 2)	ABLA/ ACGL HT (N = 3)	ABLA/ EREX HT (N = 7)	ABLA/ VAMY HT (N = 1)	PIPU/ CAFO HT (N = 3)	PIPU/ COST HT (N = 4)	ABCO/ACGL HT			ABCO/ QUGA HT (N = 1 4)	PSME/ BRCI HT (N = 2)	PSME/ FEAR HT (N = 4)
							ACGL typic P (N = 3)	Riparian P (N = 3)	BERE P (N = 5)			
<i>Abies lasiocarpa</i>												
Yng regen	25/50	3/67	18/100	3/100	•	•	•	•	•	•	•	•
Adv regen	17/50	12/100	9/86	7/100	•	•	•	•	T/20	•	•	•
Mature	3/50	4/100	3/86	3/100	•	•	•	•	•	•	•	•
<i>Picea engelmannii</i>												
Yng regen	3/50	•	20/57	37/100	•	•	•	•	•	•	T/50	•
Adv regen	4/100	1/67	7/86	28/100	•	•	•	•	T/20	•	•	•
Mature	11/100	1/33	8/100	9/100	•	•	•	•	T/20	•	T/50	•
<i>Picea pungens</i>												
Yng regen	•	•	•	•	6/100	1/50	•	•	•	•	•	•
Adv regen	•	•	•	•	10/67	7/100	•	•	•	•	•	•
Mature	•	•	•	•	4/100	6/100	•	•	•	•	•	•
<i>Populus tremuloides</i>												
Yng regen	7/50	8/33	3/43	•	11/67	10/100	2/33	1/33	1/40	T/7	T/50	T/25
Adv regen	•	1/33	4/43	•	1/67	1/75	•	•	•	•	T/50	T/25
Mature	•	T/33	1/29	•	1/67	T/25	•	T/33	•	•	•	•
<i>Abies concolor</i>												
Yng regen	•	•	•	•	•	•	6/67	8/100	9/100	26/100	•	•
Adv regen	•	2/33	T/14	•	•	•	9/100	10/100	15/100	33/100	•	•
Mature	•	1/33	T/14	•	•	•	6/100	5/100	7/80	3/79	•	•
<i>Pseudotsuga menziesii</i>												
Yng regen	•	T/33	T/14	•	12/67	5/75	4/100	•	1/60	2/64	36/100	23/100
Adv regen	•	3/100	6/29	•	7/67	2/75	5/100	•	1/80	2/64	16/100	3/100
Mature	•	6/100	1/43	•	T/33	2/75	3/100	•	3/100	T/29	11/100	4/100
<i>Pinus strobiformis</i>												
Yng regen	•	•	•	•	•	•	•	•	1/20	•	3/50	•
Adv regen	•	•	•	•	•	•	T/33	•	T/20	•	•	T/25
Mature	•	•	•	•	•	•	T/33	•	T/20	T/7	•	•
<i>Pinus ponderosa</i>												
Yng regen	•	•	•	•	T/33	•	•	•	T/20	T/29	1/50	2/50
Adv regen	•	•	•	•	T/33	•	•	•	•	3/50	T/50	5/50
Mature	•	•	•	•	T/33	•	•	•	T/20	2/71	•	3/100
<i>Pinus edulis</i>												
Yng regen	•	•	•	•	•	•	•	•	T/20	3/36	•	•
Adv regen	•	•	•	•	•	•	•	•	•	T/14	•	•
Mature	•	•	•	•	•	•	•	•	•	•	•	•
<i>Juniperus deppeana</i>												
Yng regen	•	•	•	•	•	•	•	•	•	•	•	•
Adv regen	•	•	•	•	•	•	•	•	•	T/7	•	•
Mature	•	•	•	•	•	•	•	•	•	T/7	•	•
<i>Juniperus osteosperma</i>												
Yng regen	•	•	•	•	•	•	•	•	T/20	T/14	•	•
Adv regen	•	•	•	•	•	T/25	•	•	T/20	•	•	•
Mature	•	•	•	•	•	•	•	•	•	•	•	•
<i>Juniperus scopulorum</i>												
Yng regen	•	•	•	•	•	T/25	•	T/33	•	4/43	•	•
Adv regen	•	•	•	•	•	•	•	•	•	2/36	•	•
Mature	•	•	•	•	•	•	•	•	•	•	•	•

¹Occurrence of each species in each habitat type and phase is indicated by two values separated by a slash. The first indicates the mean constancy for each species in the habitat type or phase; it is the percentage of the total number of plots in the group in which the species was found.

²Descriptions of habitat types with small sample size (N < 5) were derived as explained under Results and Discussion section.

Tree Species by Habitat Type and Phase¹

[illegible]

ity (number of stems per plot) for the tree species, averaged over all plots in the habitat type. The value to the right of the slash is the conses where a species had less than 1% cover, T is used to the left of the slash. A dot indicates that the species was not found in a group.

Species	PIEN/ Moss ² HT (N=2)	ABLA/ ACGL HT (N=3)	ABLA/ EREX HT (N=7)	ABLA/ VAMY HT (N=1)	PIPU/ CAFO HT (N=3)	PIPU/ COST HT (N=4)	ABCO/ACGL HT			ABCO/ QUGA HT (N=14)	PSME/ BRCI HT (N=2)	PSME/ FEAR HT (N=4)
							ACGL typic P (N=3)	Riparian P (N=3)	BERE P (N=5)			
Shrubs												
<i>Acer glabrum</i>	•	14/100	•	•	5/67	T/25	12/100	30/67	4/80	•	6/100	T/25
<i>Acer negundo</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Alnus tenuifolia</i>	•	•	•	•	•	4/25	•	•	•	•	•	•
<i>Amelanchier utahensis</i>	•	•	•	•	T/33	•	•	•	•	•	•	•
<i>Berberis repens</i>	•	•	T/29	•	2/100	4/100	T/33	1/66	5/80	2/79	•	1/50
<i>Ceanothus fendleri</i>	•	•	•	•	•	•	•	•	T/20	•	•	•
<i>Ceanothus integerrimus</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Cercocarpus montanus</i>	•	•	•	•	•	•	•	•	T/20	T/21	•	•
<i>Cornus stolonifera</i>	•	•	•	•	T/33	24/75	•	T/33	T/20	T/36	•	•
<i>Fallugia paradoxa</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Holodiscus dumosus</i>	•	•	•	•	•	•	T/33	•	•	T/21	T/100	1/50
<i>Jamesia americana</i>	•	•	T/14	•	•	•	•	18/67	•	•	•	•
<i>Lonicera involucrata</i>	•	•	•	•	•	T/25	•	•	•	•	•	•
<i>Pachistima myrsinites</i>	•	•	•	•	•	2/100	•	T/33	1/40	•	•	•
<i>Physocarpus monogynus</i>	•	•	•	3/100	•	•	•	•	•	T/7	•	•
<i>Prunus virginiana</i>	•	T/33	•	•	T/33	2/50	T/67	T/33	T/40	T/14	•	•
<i>Quercus gambelii</i>	•	•	•	•	•	2/75	3/67	4/67	5/60	9/93	1/50	2/75
<i>Quercus grisea</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Quercus undulata</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Ribes</i> spp.	•	•	•	•	T/100	6/75	•	•	•	•	•	T/25
<i>Robinia neomexicana</i>	•	•	•	•	•	•	T/33	T/33	T/60	T/7	T/50	T/25
<i>Rosa</i> spp.	•	•	•	•	•	T/25	•	•	•	•	•	•
<i>Rubus strigosus</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Salix</i> spp.	•	•	•	•	•	T/25	•	•	•	•	•	•
<i>Symphoricarpos oreophilus</i>	•	T/67	T/43	•	•	T/50	2/100	5/67	3/100	2/93	2/100	T/75
<i>Vaccinium myrtillus</i>	T/100	•	•	38/100	•	•	•	•	•	•	•	•
<i>Vitis arizonica</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Yucca angustissima</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Yucca baccata</i>	•	•	•	•	•	•	•	•	T/20	•	•	•
<i>Yucca schottii</i>	•	•	•	•	•	•	•	•	•	•	•	•
Graminoids												
<i>Agropyron smithii</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Andropogon gerardi</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Aristida arizonica</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Blepharoneuron tricholepis</i>	•	•	•	•	•	•	•	•	•	T/7	•	•
<i>Bouteloua gracilis</i>	•	•	•	•	•	•	•	•	•	T/7	•	•
<i>Bromus ciliatus</i>	T/50	14/100	T/57	•	1/33	T/100	4/100	T/100	12/40	T/14	45/100	1/100
<i>Carex</i> spp.	T/50	•	•	•	•	T/25	T/67	T/33	T/20	T/21	•	T/50
<i>Carex foenea</i>	•	T/33	T/71	•	16/100	13/75	•	T/33	T/20	T/14	50/100	•
<i>Carex geophila</i>	•	•	T/14	•	•	•	•	•	•	•	•	•
<i>Carex rossii</i>	•	T/33	•	•	•	T/50	3/33	•	T/80	T/43	6/100	1/25
<i>Cyperus</i> spp.	•	•	•	•	•	•	•	•	•	•	•	•
<i>Danthonia intermedia</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Elymus triticoides</i>	•	•	•	•	•	•	•	•	T/20	T/7	•	•
<i>Festuca arizonica</i>	•	•	2/43	•	3/67	T/25	•	•	•	•	T/50	14/100
<i>Festuca thurberi</i>	•	•	2/14	•	3/67	•	•	•	•	•	•	•
<i>Festuca sororia</i>	•	6/67	T/29	•	•	•	3/33	•	8/40	•	15/50	•
<i>Juncus</i> spp.	•	•	•	•	•	•	•	•	•	•	•	•
<i>Koeleria nitida</i>	•	•	•	•	T/33	T/50	•	•	T/20	T/21	•	T/100
<i>Lycurus phleoides</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Muhlenbergia emersleyi</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Muhlenbergia longiligula</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Muhlenbergia montana</i>	•	•	•	•	T/33	T/25	•	•	•	T/50	•	T/75
<i>Muhlenbergia virescens</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Piptochaetium fimbriatum</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Poa fendleriana</i>	•	•	•	•	5/67	T/50	2/33	•	T/20	T/86	T/100	2/100
<i>Poa pratensis</i>	•	•	•	•	•	•	•	•	T/20	T/7	•	•
<i>Schizachyrium scoparium</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Sitanion hystrix</i>	•	•	•	•	T/33	•	•	•	T/40	T/57	T/50	2/75
<i>Stipa</i> spp.	•	•	•	•	•	•	•	•	•	T/7	•	•
<i>Stipa pringlei</i>	•	•	•	•	•	T/25	•	•	•	•	•	•
<i>Trisetum montanum</i>	•	•	T/14	•	•	•	T/33	•	•	•	3/100	•

PSME/ MUMO HT (N=5)	PSME/ QUGA HT (N=2)	PIPO/QUGA HT			PIPO/FEAR HT			PIPO/ MUVI HT (N=3)	PIPO/ MUVI- FEAR HT (N=1)	PIPO/ MUMO HT (N=11)	PIPO/ BOGR HT (N=4)	PIPO/ Cinders HT (N=4)	PIPO/ Riparian HT (N=1)	PIPO/ Rock- land HT (N=1)
		QUGA typic P (N=5)	PIED P (N=12)	SCSC P (N=5)	FEAR typic P (N=15)	BOGR P (N=2)	QUGA P (N=2)							
.
.
.
.
2/60	5/100	2/100	1/33	T/20	T/13	.	1/50	.	5/100	1/36	.	.	T/100	.
T/20	.	T/20	T/8	T/40	T/27	.	.	T/67	T/100	T/45	T/25	.	T/100	.
.	.	.	T/42	T/25	.	.	.
.
.	.	.	T/8	9/25	.	.
.	.	.	T/8	T/25	.	.
.
T/60	1/100
.
.	.	T/20
1/40	51/100	22/100	11/100	9/80	T/47	T/50	14/100	T/33	5/100	2/82	4/75	T/50	7/100	T/100
T/40	.	.	T/8
T/40	2/50	.	T/33	T/20	.	.	.	2/67	.	T/18
.	.	.	T/8	.	T/13	T/50	T/50	.	.	.	T/25	.	.	.
T/20	.	.	T/17
.
1/40	1/50	T/20	T/8
.
.
T/20	T/50	.	T/25	T/20	.	T/50	.	T/33	.	T/27	.	.	.	T/100
.	.	.	T/17	T/20	T/20	T/50	.	.	.	T/9
.	T/7	2/25	.	.	.
.	.	.	.	T/40
T/40	.	T/40	T/25	T/40	T/13	T/50	.	.	.	T/36	T/50	T/25	1/100	T/100
.	.	.	T/58	T/80	T/7	1/100	T/50	1/100	.	T/45	14/100	T/50	.	T/100
T/40	T/50	T/20	T/17	.	T/17	T/50	.	.	T/100	T/9	.	T/50	.	.
T/20	T/50	T/40	T/33	1/60	T/27	.	1/50	T/100	.	T/36	.	.	.	T/100
T/20	.	.	T/25	.	T/7
.	T/50	.	T/17	.	.	T/50
T/80	.	T/60	T/33	T/40	2/53	.	.	.	1/100	1/64	3/50	T/50	.	.
.
.	1/100	.
.	T/50	.	T/8	.	13/93	6/100	15/100	.	12/100	.	.	.	6/100	.
.
.
T/80	.	T/60	T/67	2/100	1/73	3/100	.	T/67	1/100	1/73	2/100	T/25	1/100	.
.	3/100	.
.
100	.	2/100	1/58	8/100	5/93	5/100	12/100	T/33	.	T/9	.	.	3/100	.
.	15/100	4/100	5/100	3/75	11/75	6/100	1/100
.
1/80	2/100	3/100	4/92	3/100	2/87	6/100	T/100	T/67	1/100	2/91	2/100	4/75	.	T/100
.	T/7
.	.	.	T/17	4/100	T/7	.	.	1/100	.	T/27	.	2/75	1/100	T/100
T/80	1/100	3/100	1/92	T/100	2/80	1/100	2/100	T/100	T/100	2/100	3/100	2/100	T/100	.
.	T/18	.	.	.	T/100
.	.	T/20	T/9

Species	PIEN/ Moss ² HT (N=2)	ABLA/ ACGL HT (N=3)	ABLA/ EREX HT (N=7)	ABLA/ VAMY HT (N=1)	PIPU/ CAFO HT (N=3)	PIPU/ COST HT (N=4)	ABCO/ACGL HT			ABCO/ QUGA HT (N=14)	PSME/ BRCI HT (N=2)	PSME/ FEAR HT (N=4)
							ACGL typic P (N=3)	Riparian P (N=3)	BERE P (N=5)			
Forbs												
<i>Achillea millefolium</i>	•	T/33	T/43	•	2/100	T/75	T/67	•	T/20	•	T/50	T/25
<i>Antennaria parvifolia</i>	•	•	•	•	T/67	T/25	•	•	•	T/21	•	T/25
<i>Aquilegia elegantula</i>	T/50	T/67	T/86	•	•	•	T/33	3/33	T/40	T/7	2/50	•
<i>Aquilegia chrysantha</i>	T/50	•	•	T/100	•	•	•	•	•	•	•	•
<i>Artemisia franserioides</i>	•	•	•	•	T/33	•	•	•	4/60	•	T/50	•
<i>Artemisia frigida</i>	•	T/33	•	•	•	•	•	•	•	•	•	•
<i>Artemisia ludoviciana</i>	•	•	•	•	•	•	•	T/33	T/40	T/36	•	T/50
<i>Bahia dissecta</i>	•	•	•	•	•	•	•	•	•	•	•	T/25
<i>Brickellia grandiflora</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Campanula rotundifolia</i>	•	T/33	T/43	•	T/67	T/25	T/67	•	T/20	•	2/100	T/75
<i>Chaptalia al sophila</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Cirsium</i> spp.	•	•	T/14	•	•	•	•	•	•	•	•	•
<i>Clematis ligusticifolia</i>	•	•	•	•	•	•	•	•	9/40	T/14	•	•
<i>Clematis pseudoalpina</i>	•	•	•	•	•	•	•	1/100	•	•	2/100	•
<i>Cryptantha jamesii</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Cystopteris fragilis</i>	•	T/33	•	•	T/33	T/50	T/33	1/33	T/20	T/14	1/50	T/25
<i>Dugaldia hoopesii</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Erigeron</i> spp.	•	•	•	•	•	•	•	•	T/20	T/14	•	•
<i>Erigeron eximius</i>	T/100	2/33	T/100	1/100	1/33	•	T/33	•	T/60	•	1/50	T/25
<i>Erigeron flagellaris</i>	•	•	•	•	1/67	T/25	•	•	T/20	T/21	•	T/25
<i>Erigeron speciosus</i>	•	T/33	•	•	•	•	•	•	•	T/7	•	T/25
<i>Erigeron platyphyllus</i>	•	•	•	•	T/33	•	•	•	•	•	•	•
<i>Eriogonum jamesii</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Eriogonum racemosum</i>	•	•	•	•	•	•	•	•	•	T/7	•	•
<i>Fragaria americana</i>	•	•	T/14	•	2/67	T/50	T/67	T/67	3/60	T/50	8/50	T/25
<i>Fragaria ovalis</i>	•	•	T/29	•	T/33	T/25	T/33	•	•	T/7	•	T/25
<i>Galium boreale</i>	•	T/67	T/14	•	•	•	T/33	•	T/40	T/7	T/50	•
<i>Geranium caespitosum</i>	•	•	T/14	•	•	T/50	•	•	•	T/7	T/50	T/50
<i>Geranium richardsonii</i>	•	•	T/29	•	3/67	T/25	•	•	T/20	T/14	•	•
<i>Gutierrezia</i> spp.	•	•	•	•	•	•	•	•	•	•	•	•
<i>Haplopappus parryi</i>	•	•	•	•	T/33	T/25	•	•	6/40	T/21	T/50	T/25
<i>Helianthella parryi</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Hieracium fendleri</i>	•	•	•	•	•	T/50	•	•	•	T/7	•	•
<i>Hymenoxys</i> spp.	•	•	•	•	•	•	•	•	•	•	•	T/25
<i>Iris missouriensis</i>	•	•	T/14	•	T/33	•	•	•	•	•	•	•
<i>Ipomopsis aggregata</i>	•	•	•	•	•	•	•	T/33	T/20	T/29	•	•
<i>Lathyrus arizonicus</i>	T/100	T/100	5/86	T/100	5/100	1/75	T/67	•	T/60	T/36	1/50	2/100
<i>Lathyrus leucanthus</i>	•	•	T/14	•	•	•	•	•	•	•	8/50	•
<i>Ligusticum porteri</i>	•	•	•	•	T/33	T/50	•	•	T/20	•	1/100	•
<i>Lithospermum multiflorum</i>	•	•	•	•	•	T/25	•	•	•	T/14	•	T/75
<i>Lotus wrightii</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Lupinus</i> spp.	•	•	T/29	•	T/33	•	•	•	•	•	•	•
<i>Malaxis soulei</i>	•	•	T/29	•	•	•	•	T/67	T/60	T/29	•	•
<i>Mertensia franciscana</i>	•	T/33	•	•	T/33	T/75	T/67	T/33	T/20	T/14	3/50	T/25
<i>Osmorhiza depauperata</i>	•	1/100	T/71	•	T/33	T/50	T/100	13/33	4/40	•	8/50	•
<i>Oxalis metcalfei</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Penstemon</i> spp.	•	•	•	•	1/67	•	T/33	1/67	T/20	T/36	1/50	•
<i>Penstemon barbatus</i>	•	•	•	•	•	•	•	•	•	T/7	T/50	T/25
<i>Polemonium foliosissimum</i>	•	T/33	•	•	•	•	•	T/67	T/60	T/21	•	•
<i>Pseudocymopterus montanus</i>	T/50	•	T/71	•	3/67	•	T/33	•	T/80	T/14	2/50	T/50
<i>Pseudostellaria jamesiana</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Ramischia secunda</i>	T/100	T/67	T/57	T/100	•	•	•	•	•	•	T/50	•
<i>Senecio eremophilus</i>	•	T/33	•	•	•	•	•	T/67	T/60	T/21	•	•
<i>Senecio neomexicanus</i>	•	•	•	•	•	T/25	•	•	T/40	T/29	•	T/50
<i>Senecio sacramentanus</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Senecio sanguisorboides</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Senecio wootonii</i>	•	•	•	•	•	•	•	•	•	•	T/50	T/25
<i>Sisymbrium</i> spp.	•	•	•	•	•	•	•	•	•	T/7	•	•
<i>Smilacina racemosa</i>	•	•	T/14	•	T/67	T/100	•	1/100	T/40	•	T/50	•
<i>Smilacina stellata</i>	T/100	•	1/43	•	T/33	1/25	1/33	•	•	T/14	T/50	T/25
<i>Stellaria longifolia</i>	•	3/33	•	•	4/33	T/25	•	•	4/60	T/21	•	•
<i>Thalictrum fendleri</i>	•	T/33	T/14	•	1/100	5/100	T/67	2/100	T/100	T/71	3/50	T/25

PSEM/ MUMO HT (N=5)	PSME/ QUGA HT (N=2)	PIPO/QUGA HT			PIPO/FEAR HT			PIPO/ MUVI HT (N=3)	PIPO/ MUVI- FEAR HT (N=1)	PIPO/ MUMO HT (N=11)	PIPO/ BOGR HT (N=4)	PIPO/ Cinders HT (N=4)	PIPO/ Riparian HT (N=1)	PIPO/ Rock- land HT (N=1)
		QUGA typic P (N=5)	PIED P (N=12)	SCSC P (N=5)	FEAR typic P (N=15)	BOGR P (N=2)	QUGA P (N=2)							
T/60	T/50	T/60	T/17	T/20	2/47	.	2/100	T/67	.	T/55	.	.	T/100	T/100
T/40	.	T/40	T/33	T/40	T/53	T/50	T/100	.	T/100	T/45	T/25	T/25	.	.
.
.
.	T/7
T/60	.	T/40	T/42	T/40	.	.	T/50	.	.	T/18	T/50	.	.	.
T/40	.	T/60	T/17	T/40	T/13	.	.	T/33	.	T/36	.	T/75	.	T/100
T/40	T/50	.	.	T/20	T/13	T/50
.
.	.	T/20	.	T/40	.	.	2/50	.	.	T/36	.	T/25	.	.
.
.
.	.	.	.	T/7	T/50	T/75	.	.
.	.	.	T/17	.	.	T/50	.	.	.	T/9
.	.	T/20	T/17	T/20	T/25	T/25	.	T/100
.	T/7
T/20	.	.	T/33	T/40	T/40	T/50	T/100	T/33	.	T/36	T/100	.	T/100	.
T/80	1/50	T/20	T/17	T/20	T/33	T/50	.	.	.	T/45
.	.	T/20	T/9
T/20	.	.	.	T/20	.	T/50	.	T/33
.	.	T/40	T/50	T/40	T/7	T/50	.	.	.	T/18	1/50	.	.	.
T/20	2/50
T/20
T/20	T/50	.	T/8	T/9	.	.	T/100	.
T/40	.	.	T/25	.	T/7	.	T/50	T/33	.	T/27	T/25	T/50	T/100	.
T/20	T/7
T/20
T/20	.	.	T/8
T/20	1/100
T/40	.	.	T/8	T/40	T/27	.	T/50	T/67	T/100	T/36	.	T/25	.	.
T/20
.	.	T/40	T/17	T/40	T/27	.	.	T/33	.	T/45	T/50	T/75	T/100	.
T/40	2/50	.	T/17	T/20	T/13	.	3/100
.
.	T/50
T/60	.	T/80	T/25	T/60	T/20	.	.	.	T/100	T/27	.	T/75	T/100	.
T/20	.	T/60	T/25	T/40	T/33	.	.	T/100	T/100	T/55	T/25	T/75	.	.
T/20	.	T/20	.	.	T/13	T/9	.	T/25	.	.
.	.	T/20
T/40	2/50	T/20	T/9
.	.	.	T/8
.
T/20	.	.	T/42	T/40	T/13	1/18	T/50	T/25	T/100	T/100
.	T/50	T/20	T/25	.	T/20	.	.	T/33	.	T/18	.	T/50	.	.
T/80	.	T/60	.	T/40	T/73	T/50	3/100	T/33	T/100	T/45	.	T/25	T/100	.
.
.
T/60	T/50	T/80	T/67	T/80	T/67	T/50	.	T/100	T/100	T/64	T/50	T/50	T/100	T/100
.
T/20	.	T/20	T/8	.	T/7
T/40	T/50	T/20	T/17	T/80	T/20	T/55	T/25	T/50	.	T/100
.	T/50
.
T/60	T/50	T/40	T/42	T/20	T/7	T/27	.	T/25	T/100	.

Species	PIEN/ Moss ² HT (N=2)	ABLA/ ACGL HT (N=3)	ABLA/ EREX HT (N=7)	ABLA/ VAMY HT (N=1)	PIPU/ CAFO HT (N=3)	PIPU/ COST HT (N=4)	ABCO/ACGL HT			ABCO/ QUGA HT (N=14)	PSME/ BRCI HT (N=2)	PSME/ FEAR HT (N=4)
							ACGL typic P (N=3)	Riparian P (N=3)	BERE P (N=5)			
<i>Thermopsis pinetorum</i>	•	•	T/14	•	T/33	T/50	•	•	•	T/7	•	•
<i>Valeriana</i> spp.	•	•	•	•	•	•	•	•	•	•	•	•
<i>Valeriana capitata</i>	•	•	•	•	•	•	1/100	T/33	•	T/14	13/50	•
<i>Vicia americana</i>	•	1/33	3/43	•	6/100	T/100	T/67	•	1/60	T/21	2/50	T/100
<i>Viola canadensis</i>	T/50	T/33	T/29	•	T/67	T/50	T/33	2/33	1/60	•	T/50	T/25

¹Occurrence of each species in each habitat type and phase is indicated by two values separated by a slash. The first indicates the mean constancy for each species in the habitat type or phase; it is the percentage of the total number of plots in the group in which the species was

²Descriptions of habitat types with small sample size (N = <5) were derived as explained under Results and Discussion section.

PSEM/ MUMO HT (N=5)	PSME/ QUGA HT (N=2)	PIPO/QUGA HT			PIPO/FEAR HT			PIPO/ MUVI- FEAR HT (N=3)	PIPO/ MUVI- FEAR HT (N=1)	PIPO/ MUMO HT (N=11)	PIPO/ BOGR HT (N=4)	PIPO/ Cinders HT (N=4)	PIPO/ Riparian HT (N=1)	PIPO/ Rock- land HT (N=1)
		QUGA typic P (N=5)	PIED P (N=12)	SCSC P (N=5)	FEAR typic P (N=15)	BOGR P (N=2)	QUGA P (N=2)							
•	•	•	•	T/20	•	•	•	•	•	•	•	•	T/100	•
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
•	T/50	T/20	T/8	T/20	T/20	•	T/100	•	•	T/9	•	•	•	•
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•

coverage (in percent) for the shrubs, grasses, and forbs, averaged over all plots in the habitat type. The value to the right of the slash is the found. In cases where a species had less than 1% cover, T is used to the left of the slash. A dot indicates that the species was not found in a group.

Alexander, Billy G., Jr., E. Lee Fitzhugh, Frank Ronco, Jr., and John A. Ludwig. 1987. A classification of forest habitat types of the northern portion of the Cibola National Forest, New Mexico. USDA Forest Service General Technical Report RM-143, 35 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Forest habitat types in the Cibola National Forest (except the Magdalena District) of New Mexico were identified and described to develop an ecosystem classification based on potential natural vegetation. The final classification utilized data from 124 sample plots. A total of 6 climax series, 21 habitat types, and 9 phases of habitat types are defined. Keys and descriptions for each habitat type are provided. Vegetational relationships, physical settings, and relationships to adjacent habitat types and other habitat type investigations in the Rocky Mountains are discussed.

Keywords: Forest vegetation, New Mexico, habitat types, plant communities, plant associations, forest ecology, forest management.



Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
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Rocky Mountain Forest and Range Experiment Station

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*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526



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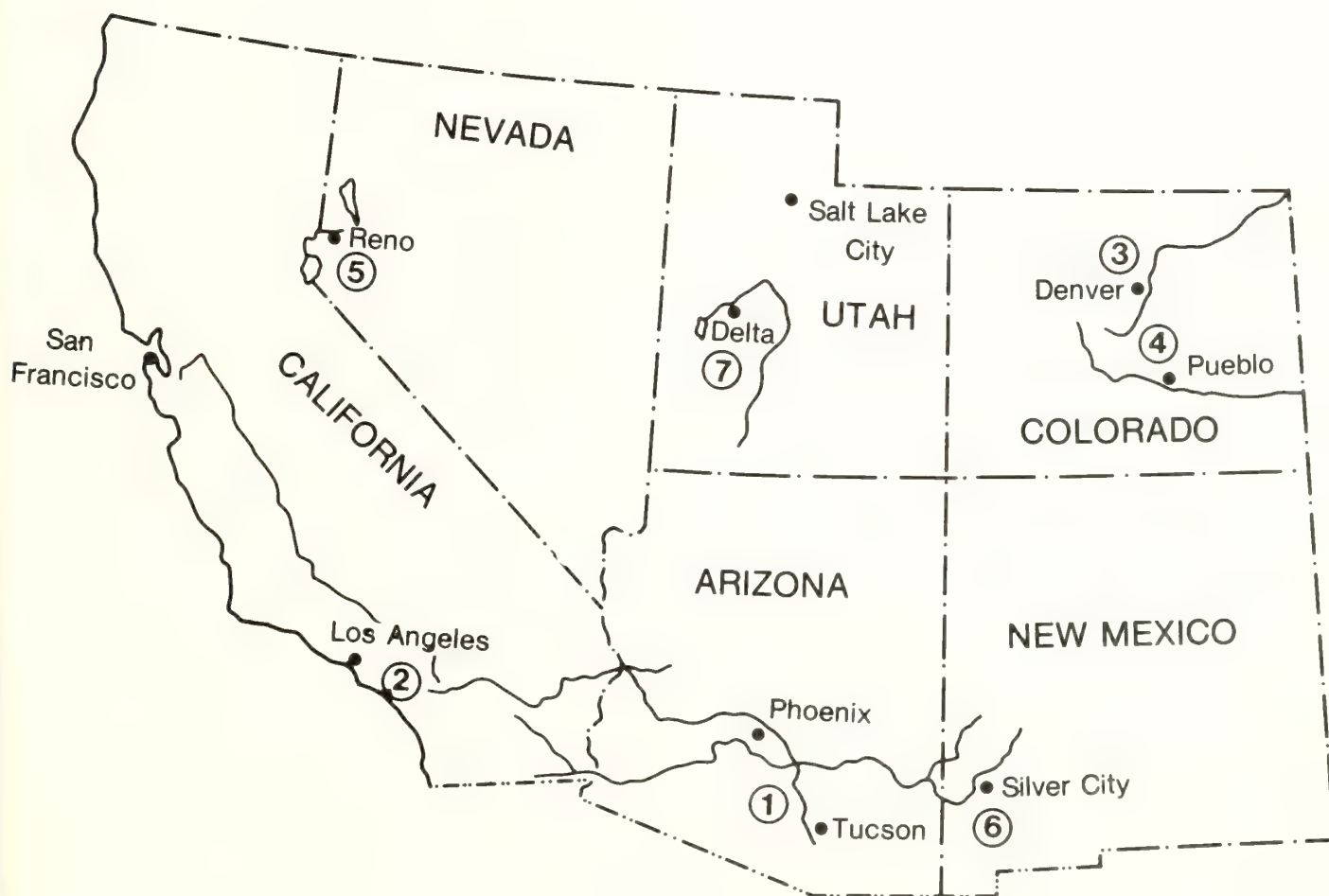
Fort Collins,
Colorado 80526

General Technical
Report RM-144



Water Marketing in the Southwest— Can Market Prices Be Used to Evaluate Water Supply Augmentation Projects?

Bonnie Colby Saliba, David B. Bush, and William E. Martin



Abstract

Price behavior over time in selected western water markets is observed and assessed as a useful measure of the economic value of water. Market characteristics that may distort prices include imperfect competition, third-party effects, institutional and hydrologic uncertainty, and equity considerations. Nonmarket valuation techniques are useful in supplementing market price information.

Acknowledgements

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Water Marketing in the Southwest— Can Market Prices Be Used to Evaluate Water Supply Augmentation Projects?

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Bonnie C. Saliba, David B. Bush, and William E. Martin

MANAGEMENT IMPLICATIONS

Valuation of incremental changes in water availability is an important issue in the Western United States as agriculture, industry, energy development, and population growth exert increasing pressure on limited water resources. Water yields can be significantly increased by management practices on public lands, raising questions regarding the value to society of these potential increments. Strong pressures for marketing water exist as water in many regions is fully appropriated and new uses can be accommodated only through transfer from established uses. In some areas, market activity has been occurring for several decades. In others, institutions that govern water allocation are only slowly becoming receptive to the market transfer of water rights. This report analyzes selected water markets in the Western United States by measuring water prices over time and by evaluating the appropriateness of market prices as measures of the economic value of incremental increases in water supplies.

Equity issues, external effects of market activity, imperfect competition, and legal, economic, and hydrologic uncertainty are identified as market characteristics that may distort prices as indicators of water values. Western water markets exhibit these characteristics to varying degrees, and the appropriateness of using a particular set of prices must be evaluated case by case, based on a thorough understanding of market activities and price formation processes. Even if there are no conceptual reasons to question whether observed prices are appropriate measures of value, there are a number of practical problems in using market prices. Prices are rarely a matter of public record and price data must often be elicited from market participants. Several types of water commodities and market prices are found in each of the regions studied, and it must be determined which, if any of them, are appropriate for valuing augmented yields.

Market prices will not usually provide an appropriate measure of value for public decision-making and should be used as one of several sources of information on water values. Under most circumstances, nonmarket valuation techniques would be helpful in supplementing price data generated by market transactions. Use of both market and nonmarket information is recommended to ensure that agencies seeking to value increased water supplies use measures that approximate willingness to pay for additional water.

INTRODUCTION

RESEARCH OBJECTIVES AND SCOPE

Public agencies are often faced with the task of estimating costs and benefits associated with water supply augmentation projects. Proposed projects may include construction of water storage and delivery facilities or, in the case of the Forest Service, U.S. Department of Agriculture, changes in land management practices that will alter the quantity and timing of water yields. One of the difficulties in estimating project benefits involves assigning an appropriate value to increments in water supply attributable to the project. The broad purpose of this research was to investigate water markets in the Southwest and, based on that investigation, to evaluate the usefulness of market water prices as measures of value for public project evaluation and water policy development.

To accomplish this overall purpose the research had several major objectives:

- Describe and compare the legal institutions relevant to market transfers of water in Arizona, California, Colorado, Nevada, New Mexico, and Utah.
- Identify and describe water markets in selected study areas.
- Analyze and compare markets in terms of historical development, supply and demand, structure, and the competitiveness of the price determination process.
- Compile data, where available, on water prices over time in selected markets.
- Evaluate the appropriateness of using market prices as measures of the economic value of incremental changes in water supplies.

Descriptions and comparisons of selected water markets and observed price data are presented. Theoretical and practical considerations that affect the appropriateness and usefulness of observed prices as measures of value for use by public agencies are discussed. Prices generated within the water markets investigated in this study are evaluated and analyzed. Implications for valuing incremental water yields from public lands are summarized. Finally, recommendations are offered on the use of market prices by public agencies, as well as suggestions for future research efforts complementary to the objectives and results of this study.

GENERAL CHARACTERISTICS OF SOUTHWESTERN WATER MARKETS

A water market may be defined as any institutional setting within which the right to use water is bought, sold, rented, or traded among consenting parties. Water rights are frequently transferred incidentally as a part of a transaction involving land, improvements and other goods. However, this research focuses on areas where water rights are recognized as having independent value and where transfer of water rights is the primary purpose of transactions involving water. Western water markets are generally in a rudimentary state of development compared to markets for other natural resources, such as land, natural gas, timber, or minerals. Markets often have poorly developed channels for communicating information on prices and sales, and for bringing potential buyers and sellers together. Even in areas where active and well-developed markets exist, only a small proportion of total water supplies are likely to be included in market transactions. Federal project water, a significant proportion of water supplies in many areas, has not been readily transferable and usually is not priced to reflect local water values.¹ It is provided on a contractual basis at rates that will cover project repayment obligations only.

Water markets operate in the broad context of western water law and institutions. Several common characteristics serve to distinguish water institutions in the Southwest from other regions in the United States. Water use in the Southwest has been dominated by irrigated agriculture. Early settlement in the Southwest centered around primary industries such as mining, ranching, and agriculture. Irrigated agriculture currently represents a minor portion of the income generated in many Southwestern States. Yet, this sector is still the predominant user of water throughout the region.

Irrigated agriculture (and to a lesser extent, mining) generated demand for water that the seasonal and unpredictable surface water resources of the Southwest could not satisfy. Water users built systems to capture, store, and transport water to bring it to where it was demanded, at the proper time and in the desired quantities. The pattern of water resource development reflected a fundamental reality of the arid West—potentially productive lands frequently were located distant from riparian areas. Typically, water diverted and stored at only a few strategic locations along a stream system supports a network of users located miles away from the source.

Separation between the point of diversion and the place of use grew ever wider when state and federal governments began ambitious land and reclamation programs early in the 20th century. As “native” sources of water were developed, water was transported across greater distances. Systems of pipes, pumps, reservoirs, and canals permitted the transportation of tens or even hundreds of thousands of acre-feet of water per year across mountain ranges and entire hydrologic basins to areas of growing water demand.

Increasing development of limited water resources led to conflicts among competing water users. Coincident

with the physical development of water resources, laws and institutions evolved to address the issues of ownership, access, and water rights distribution peculiar to the Southwest. English common law and riparian system of water rights, predicated on a close association between water resources and the land from which they originated, were poorly suited to the arid conditions that influenced water resources development and use in the West. Riparian water law was inappropriate for development of water resources in the West, because it provided for the use of water at locations adjacent to water sources only. The legal doctrine of prior appropriation, first developed by miners in California during the gold rush of 1849, soon became almost universally accepted throughout the West as the legal basis for defining and allocating property rights in water. Under the appropriation system, water could be withdrawn from the water source and used in distant locations. Water rights were defined not in terms of the ownership of land adjacent to a watercourse, but in terms of “beneficial use.” That is, the use to which water was put defined the extent of a user’s property right in water.

The Southwestern States have experienced rapid rates of population and economic growth since the Second World War. Concurrent with this growth, there has also been a significant structural change in regional economics. While irrigated agriculture remains the predominant water user region-wide, the nonagricultural sectors of the economy now employ all but a fraction of the work force and earn the great bulk of all income. The construction, manufacturing, service, and government sectors of the economy are competing for land and water resources once predominantly devoted to agriculture.

Until fairly recently, the role of state, regional, local, and private water organizations was two-fold — first, to develop water resources and acquire water rights, and then to ensure that the distribution and use of those rights among the water users concerned was fair and equitable. It was not, however, the primary responsibility of water organizations to ensure that water use also was efficient. So long as water supplies were inexpensive to develop, undeveloped resources remained abundant, and grossly wasteful practices avoided, water users were largely insulated from outside pressures to put their resources to the best economic use.

The western water economy in the second half of the twentieth century has been characterized by rapidly rising water costs. Demands for federally funded water projects grew in size, sophistication, and cost as ever larger amounts of public capital were required to draw water from increasingly less accessible sources. The era of cheap and abundant western water has ended. The federal government is increasingly reluctant to commit funds to projects whose costs continue to spiral upwards. Total costs for the Central Utah Project are estimated to approach \$1.8 billion.² The Animas-La Plata Project was pushed through Congress only after the original design was scaled down considerably, from a cost in excess of \$800 million down to an estimated \$572 million.³ The Central Arizona Project, touted as one of the last and greatest of federal water projects, will cost over 3.3 billion dollars to complete.⁴

Emphasis in public water resource policy has begun to shift from supply enhancement towards supply and demand management. A report prepared in 1986 for the Western Governors' Conference stated that "the most effective role of the U.S. Bureau of Reclamation is changing from one of supplying capital for large new water projects to helping the West enhance the efficiency of use of the water that the Bureau already provides."⁵ Similar conclusions might be drawn about the changing roles of state and local governments and private water agencies. As quantities of available new water supplies diminish, interest in improving the efficiency of use of existing water supplies grows. One of the most effective means of improving the efficiency of water use is to reallocate supplies from relatively inefficient or low-valued uses to more efficient, higher-valued uses. Increasing demand for flexible mechanisms to optimally reallocate existing water resources has led to an exploration of the potential for decentralized reallocations through voluntary market exchanges.

In some areas of the Southwestern United States, water market activity has been occurring for some time. In other areas, institutions are only now starting to respond to pressures for market transfers of water. This report describes and evaluates the structure, prices and institutional characteristics of specific southwestern water markets.

The general study area for the project, which covers the arid and semiarid regions of the Southwestern United States, includes the States of Arizona, California, Colorado, Nevada, New Mexico, and Utah. Within each state one or two "market areas" were identified for in-depth study. These areas are shown on figure 1. Four basic criteria were used to select the market areas.

First, each area needed to have well-defined geographical boundaries. The water markets studied exist within relatively closed systems, though none is absolutely closed to the transfer of water into or out of its areas.

Second, each market was characterized by an economic scarcity of water resources. If water were available to meet all potential demand at prevailing prices and costs of obtaining water there would be no incentive for market activity. The scarcity criteria did not limit the study to areas in which absolutely no additional water

resources could be appropriated. Some market areas investigated remain open to either limited new appropriations or to the importation of additional water supplies. In each of these markets, however, new water rights are generally either (1) restricted in quantity or purposes of use, (2) legally difficult to obtain, or (3) prohibitively expensive to develop. Therefore, purchase of existing water rights is an attractive option to users desiring additional water.

Third, active markets with some history of water transfers continuing up to the present time were selected. Locations with low levels of activity were of less interest because of sporadic price data. The observation of both changes in market structure and price levels over time is an important means of evaluating market processes.

Finally, it was important that information on market transactions be available. Some areas were rejected because the records on market transactions were too dispersed, too difficult to obtain, and/or too poorly maintained to provide meaningful information.

DESCRIPTION OF DATA

Lack of secondary sources containing detailed price observations necessitated extensive fieldwork. A major source of information was price data obtained from individuals familiar with market transactions.

An effort was made in the study to render all price observations uniform and comparable over time. Unless otherwise indicated, all prices were adjusted, using the Gross National Product (GNP) price deflator, to equivalent 1986 dollar values. The uniformity of price observations is affected by the definition of the water commodity being traded. Several conventions were adopted in this report in order to clarify the meaning behind the comparison of prices among various water rights.

Water rights may be transferred in perpetuity (sold) or temporarily (rented). The transfer of a perpetual water right gives the holder access to water resource indefinitely, that is, the right is bought or sold. A temporary, or seasonal transfer gives the holder access to the water resource for only a certain length of time, that is, the right is leased or rented. Most transactions described in this study were sales of perpetual water rights.

It is important to distinguish between the right of diversion and the consumptive use portion of a water right. Diversion rights refer to the maximum quantity of water that may be drawn for use. Consumptive use refers to the portion of that diversion right that may be removed permanently from the hydrologic system. Under many systems of water law, only the consumptive use portion of a water right may be transferred, that is, the historical level of return flows occurring in the system of origin cannot be reduced as a result of the transfer. Unless otherwise indicated, all transfers described in this report refer to the maximum quantity of water the buyer is allowed to divert. If the described transfer has only been proposed but is not yet in effect, then the quantity described usually refers to the quantity historically diverted by the prospective seller.

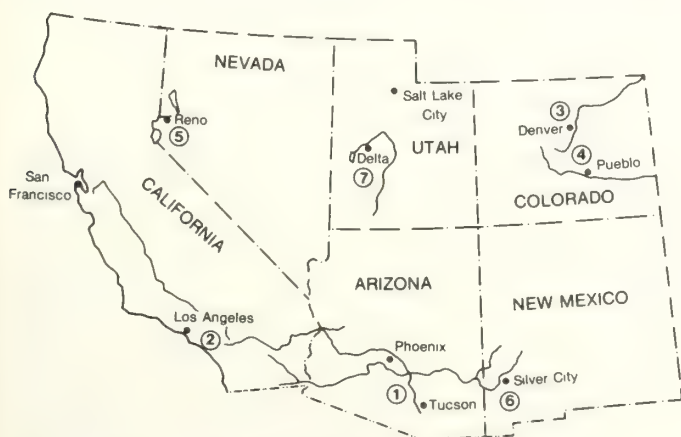


Figure 1.—Southwestern water market study areas.

Water rights are quantified by flow rate or by volume, and sometimes in terms of both. Flow rate measures are usually expressed in cubic feet per second, while volumetric limits are most often measured in acre-feet (over a fixed period of time, usually a year). Unless otherwise indicated, all transfers are expressed in terms of acre-feet per year.

Water rights are usually limited by a specified maximum level of diversion, but hydrological shortfalls or the system of established priorities among water rights may prevent a right from producing its maximum potential yield. In addition to the allowable level of diversion, therefore, prospective buyers of water rights may also be concerned with the long-term average expected yield, the minimum possible ("firm") yield, and the variability of the yield. Wherever possible, in this report water rights transfers are quantified in terms of the known long-term average yield.

MARKET DESCRIPTIONS AND COMPARISONS

SOUTHERN ARIZONA

Description of the Study Area

The Arizona market areas studied are the Tucson and Phoenix Active Management Areas (AMAs), two of the four AMAs created under the Arizona Groundwater Management Act of 1980. The Phoenix AMA includes the Phoenix metropolitan area and most of Maricopa County. The Tucson AMA includes the Tucson metropolitan area and parts of Pima, Pinal, and Santa Cruz counties. Figure 2 shows the AMAs along with the Central Arizona Project aqueduct.

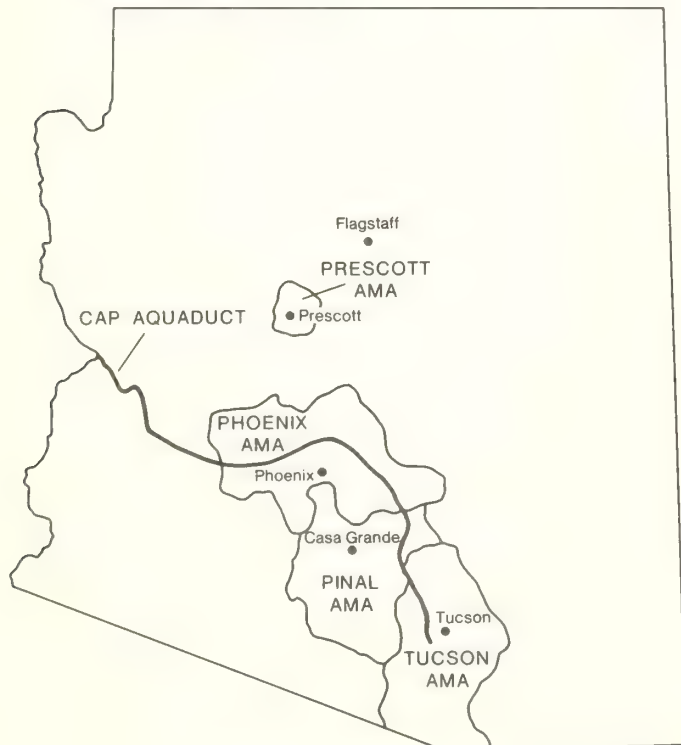


Figure 2.—Southern Arizona.

Approximately 60% of Arizona's annual average water usage (roughly 8.2 million acre-feet) is derived from groundwater sources. The remaining 40% comes from developed surface water sources.⁶ The Salt River Project (SRP) provides substantial quantities of surface water from the Salt and Verde Rivers for users in the Phoenix AMA. Phoenix area surface water supplies are supplemented with groundwater pumping. In contrast, water users in the Tucson AMA are completely dependent upon groundwater pumping for their supplies. Available water supplies in both AMAs will increase as Colorado River water is delivered via the Central Arizona Project (CAP). Limited CAP deliveries began to the Phoenix area in 1985, and the project will begin serving the Tucson area in the early 1990s.

Over 85% of the annual water supply in Arizona is currently used by irrigated agriculture.⁶ The number of irrigated acres in the State peaked in the early 1960s, and since then has been shrinking as farmland is retired for urban development. While agriculture has declined in economic importance, the nonagricultural sectors of the economy around Tucson and Phoenix are expanding at a rapid pace.⁷

The CAP has changed in purpose and function over time as the political economy of water in Arizona has changed. As originally conceived, it was meant to be a supplemental water supply for irrigation in Central Arizona. By the time construction of the aqueduct reached its midpoint in the early 1980s, the project had become a component of a comprehensive state program of conserving scarce groundwater resources for urban development. Recently the CAP has begun to assume an additional role as a mechanism for water transfers from agriculture to urban users. The 300-mile-long canal links Phoenix to the Colorado River and, when completed, will convey water all the way to Tucson. The aqueduct connects scattered Arizona groundwater and surface water systems where no such linkage existed before. Several proposals are currently under evaluation by the cities of Phoenix, Scottsdale, and Mesa and several private enterprises to use the CAP for interbasin water exchanges and transfers all across central Arizona.

Water Laws and Institutions

Surface Water Rights

Arizona has a dual system of water rights. Surface water rights were developed under the appropriation doctrine common to the Western United States. Groundwater rights, however, are managed under a permit system.⁸

Before 1962, appropriative rights to surface waters were not transferable by their holder to locations other than those specified in the original granting of the right. The only exception arose when the original site was destroyed or impaired by natural calamity. Under such circumstances the right could be moved with the approval of the appropriate administrator or by court order. In 1962 this legal constraint was removed and surface

water rights became transferable, in principle, to new locations provided that the rights of existing appropriators were not impaired. However, transfers continue to be hindered by numerous legal and hydrologic limitations and few have actually taken place.⁷

Groundwater Rights

The passage by the Arizona legislature of the Groundwater Management Act of 1980 accomplished three purposes. First, it created a Department of Water Resources to regulate water resource development and use in the State. Second, it explicitly defined and qualified groundwater rights. Third, it established an agenda for groundwater management.

Under the Act four administrative regions, or Active Management Areas (AMAs), were created under the Department of Water Resources to grant and manage water rights as defined in the legislation and to establish and administer water conservation and supply augmentation programs. The objective of the water conservation and supply augmentation plans is to eliminate virtually all groundwater overdraft in Arizona by the year 2025.

There are four basic classes of legally recognized groundwater rights within the AMAs—exempt withdrawals, grandfathered rights, service area rights, and groundwater withdrawal permits. Withdrawals of groundwater for nonirrigation domestic uses from wells with pump capacities of not more than 35 gallons per minute, or for non-irrigation commercial uses not exceeding 10 acre-feet per year, are exempt from most regulation under the law. Nonirrigation uses include the irrigation of less than 2 acres of land. Individuals may continue to appropriate water for exempt purposes in AMAs, so long as they conform to rules on groundwater well spacing. These regulations are intended to mitigate the adverse impact that a new well could have on nearby groundwater pumpers.

There are three types of grandfathered rights (GFRs): irrigation GFRs, Type I nonirrigation GFRs, and Type II nonirrigation GFRs. An irrigation GFR applies to two or more acres irrigated for the purpose of growing plants for sale or human consumption or to use as feed for livestock or poultry. Irrigation GFRs may be converted to nonirrigation use, but no other water right may be converted to an irrigation GFR. Irrigation GFRs are limited to lands irrigated during the historical period January 1, 1975 to January 1, 1980.

The quantity of an irrigation water right on a particular parcel of land is formulated by the local AMA on the basis of three factors: the water duty per acre, the number of grandfathered acres, and the number of water duty acres. The irrigation water duty is a measure of water use per acre, based on the historical period January 1, 1975 to January 1, 1980. The number of water duty acres is the maximum number of grandfathered irrigation acres that were irrigated during any one of the eligible years. Because of crop rotation practices, the number of water duty acres may be significantly less than the total number of grandfathered irrigation acres.

The maximum quantity of water that may be used per grandfathered irrigation acre is the product of the water duty and the ratio of the number of water duty acres to the number of grandfathered acres. (For example, if the water duty is equal to 4 acre-feet per acre, and there are 80 water duty acres and 100 grandfathered irrigation acres, the maximum water allowance per grandfathered irrigation acre is $4 \times (80/100) = 3.2$ acre-feet). Irrigators may choose in any year to irrigate all of their grandfathered irrigation acres and spread out their water rights, or they may irrigate fewer acres and concentrate their water use. The 1980 Groundwater Management Act mandates that water conservation requirements must increase over time. Each AMA will progressively reduce irrigation water duties. Because the number of grandfathered and water duty acres on any given parcel of land will not increase, the total water available for irrigation will gradually diminish.

Type I non-irrigation GFRs apply to farmland retired from irrigation after January 1, 1965 in anticipation of a specific non-irrigation use. Type I GFRs recognized in 1980 with the passage of the Groundwater Management Act are granted 3 acre-feet per acre. A Type I right converted from a retired grandfathered irrigation right subsequent to 1980 allows a right-holder to pump the lesser of 3 acre-feet of groundwater per acre from the retired land or the maximum water allowance per grandfathered irrigation acre.

Type II non-irrigation GFRs apply to non-irrigation withdrawals of groundwater that occurred when the AMAs were established. Generally the quantity of water assigned to a Type II right equals the maximum amount of water withdrawn and used for non-irrigation purposes in any 1 of the 5 years before the designation date of the AMAs. No new Type II rights may be created after the designation of an AMA.

Cities, towns, private water companies, and irrigation districts have “service area rights” to withdraw and transport groundwater. The groundwater law defines the service area of a city, town, or private water company as the area of land actually served by the entity and any additional areas that contain an operating distribution system owned by the entity and used primarily for the delivery of non-irrigation water.

A city, town or private water company has the right to withdraw as much groundwater from within its service area as it needs to serve the residents and landowners within the service area. The quantity of water legally available to a service area is therefore not fixed and may expand over time. However the state plans to limit the expansion of service area rights through mandatory reduction in per capita water use within each service area.

Those who are not eligible for GFRs or service area rights may obtain the right to withdraw and use groundwater for new or expanded nonirrigation purposes by applying for a temporary groundwater withdrawal permit. If certain criteria are met, the Department of Water Resources may issue such permits. Groundwater withdrawal permits specify limits on both the duration and quantity of withdrawals.

In addition to appropriated surface water rights and permitted groundwater rights, there are two other types of water rights available within AMAs—CAP water and sewage effluent. CAP water is available to a local water service organization, on a contractual basis, through the Central Arizona Water Conservancy District, which serves as a liaison with the Bureau of Reclamation. Water users may not freely transfer CAP water among themselves, although land with CAP water service contracts may be bought and sold. Subcontracts for agricultural CAP water may be converted to municipal and industrial water service subcontracts at the rate of 1 acre-foot per acre.⁹

A water user who wishes to acquire new or additional groundwater rights but for whom exempted groundwater rights or temporary groundwater permits are not feasible, may lease or purchase a GFR. Most permitted rights issued pursuant to the 1980 Code may be transferred, but they are usually only available for the same type of use. The major exception to this rule is the convertibility of an irrigation GFR to a Type I non-irrigation right. All transfers are subject to certain restrictions and must be approved by the Department of Water Resources. Temporary use permits may not be transferred.

Grandfathered irrigation rights are appurtenant to the land for which the right was granted and may not be severed from that land. The full amount of the water right is transferred with the ownership of the land. Grandfathered irrigation water may not be used for any purpose except irrigation and livestock watering. The water rights may only be used on the land for which the right was granted or on contiguous acreage under common ownership. The only exception to the strict appurtenancy rule for grandfathered irrigation rights is that a landowner may petition to substitute flood-damaged acres for other irrigation acres and transfer the water right.

Type I non-irrigation rights, or grandfathered irrigation rights that have been converted into Type I non-irrigation rights, are also strictly appurtenant to the land where the right originated. The full amount of the right is conveyed with the sale of the land. However, any quantity of water up to the limit of the right may be transported off the land to non-irrigation uses in other locations. Type I water may be transported within, between, or outside existing AMAs without liability or injunction.

If a Type I right has been converted from an irrigation right, the irrigated land must be permanently retired from irrigation. The number of acre-feet of water assigned to the Type I right is determined at the time of the conversion to non-irrigation use and remains fixed at that quantity for all future conveyances. Type I water may not be used for irrigation, and the right cannot be converted back to a grandfathered irrigation right.

Type II non-irrigation rights are the only groundwater rights not strictly appurtenant to a particular parcel of land. Within any given AMA, Type II rights may be freely transferred, subject only to legal regulations concerning the spacing of groundwater wells.¹⁰

Type II rights may not be used for irrigation, and are limited in the range of non-irrigation uses to which they

may be put; rights designated for use in power generation or for mineral extraction are confined to those specific uses. Probably the greatest limitation on the transferability of a Type II right is its indivisibility; the law does not permit splitting Type II rights up into two or more smaller rights.

Effluent

In recent years treated sewage effluent has begun to receive increasing attention for its potential in conserving water through exchanges of potable for nonpotable supplies, satisfying Indian claims to water rights, recharging groundwater aquifers, and as a marketable resource.¹¹ Only small quantities of effluent have been bought and sold in Arizona to date, but management and marketing strategies are being discussed actively.

The legal status of effluent ownership, use, and transfer in Arizona is not yet clear. A major unresolved question concerns whether or not effluent is subject to regulation under state laws governing surface water appropriation and groundwater management.¹² A state court has declared that effluent is neither groundwater nor surface water and is not subject to existing state water law. If this decision is not reversed then effluent may be one of the most marketable water commodities in Arizona.

Water Market Activity

Water market activity in southern Arizona includes transactions involving Type I and Type II groundwater rights, adjudicated surface flows, and sewage effluent. One of the oldest water markets in Arizona is Tucson's ongoing acquisition of irrigated farmland in the Avra Valley, which lies about 15 miles to the west of the city. Tucson had contemplated developing water rights in the valley since at least the 1940s. The city acquired parcels of land and developed a wellfield and a transmission system to convey the water into the city in the mid-1960s. Transportation of Avra Valley water into the Tucson basin began in 1968.¹³

In 1971 Tucson began purchasing additional land in the Avra Valley in the vicinity of its wellfields. Over the 8-year period from 1971 to early 1979, Tucson acquired over 13,000 acres of irrigated land and brought farming to an end in the southern end of the Avra Valley. In 1979, when the passage of new water management legislation in the State was imminent, the Tucson city council called a moratorium on further land acquisitions until the legal status of their acquisitions could be clarified. Tucson ended the moratorium in 1984, and by the close of 1986 another 7,000 acres of farmland had been purchased and retired. The city expects to acquire the remaining 20,000 acres of privately owned irrigated land in the central and northern portions of the Avra Valley over the next 10 years.¹⁴

At the legal maximum of 3 acre-feet of water rights per grandfathered irrigated acre per year, Tucson's water right holdings in Avra Valley are in excess of 55,000 acre-feet per year. This is equal to nearly two-thirds of the annual level of water usage in the city. In recent years

Tucson has been pumping only between 5,000 and 6,000 acre-feet per year from the Avra Valley wellfields. Pumpage is expected to rise to over 15,000 acre-feet per year before the arrival of CAP water in the early 1990s. Pumpage will then decline to about 2,000 or 3,000 acre-feet per year, the minimum required to meet peak load demands on the city's water system. Importation of Avra Valley water is projected to increase again in future years as Tucson's population continues to increase.¹⁴

Prices for land purchased in Avra Valley have ranged between \$1,000 and \$2,000 per acre. Slightly more than 75% of the land Tucson has acquired in the Avra Valley has irrigation water rights. The city spends about \$150,000 per year to reduce dust and weed problems on its retired farmlands,¹³ in addition to the cost of acquiring land and water rights in the Avra Valley. If one assumes that the land and improvements have no value once the appurtenant irrigation rights have been retired for city use and that the transferable water rights average 3 acre-feet per acre of irrigated land per year, then current purchase prices for water rights range between \$650 and \$850 per acre-foot.

A second example of the acquisition of farmland for the conversion of grandfathered irrigation rights to Type I non-irrigation rights involves the city of Mesa, located in the Phoenix AMA. In the spring of 1985, Mesa purchased over 11,500 acres of irrigated farmland in fourteen separate transactions. The farmlands have irrigation GFRs which may be converted to Type I non-irrigation GFRs with a yield of over 30,000 acre-feet per year. They lie approximately 40 miles to the south of Mesa in neighboring Pinal County (Pinal AMA). Mesa intends to lease the land back to farmers for about 5 to 15 years, until the city is ready to develop the water rights for municipal use. The total cost of purchasing the 11,500 acres of land and 30,000 acre-feet of water rights was over \$29 million. Prices ranged between \$1,900 and \$3,000 per acre, with an average price of about \$2,600 per acre. Assuming the land has no value without the water rights, Mesa paid an average of about \$1,000 per acre-foot.

If necessary, Mesa is willing to pipe the groundwater all the way to the city from the retired farmland. As a less costly alternative, however, Mesa is attempting to get approval from the Department of Water Resources for a plan to exchange groundwater for CAP water. Under this plan the city would pump Type I groundwater from the retired farmland into the CAP aqueduct, where it would then flow south to Tucson. In exchange, Mesa would pick up an equal quantity of CAP water (water meant originally for Tucson) out of the city's diversion point from the CAP aqueduct. Mesa does not yet have cost estimates for alternative proposals to deliver (or exchange) water to city users.¹⁵

The magnitude of Mesa's purchase has given rise to numerous concerns in Pinal County about the local economic impact of the farmland sales; primarily, the effect of the farmland sales on the tax base, and the loss of available water for development. Mesa hopes to allay these concerns by actively supporting the local community. In addition to the cost of purchasing the land and water rights, Mesa has committed itself to making

"in lieu of taxes" payments to the two irrigation districts within which the farms are located. The city is also negotiating to keep the farmland's CAP allocation of 1 acre-foot of water per acre on the land for urban and industrial development.¹⁶

Type II non-irrigation grandfathered rights have been bought and sold in both the Phoenix and Tucson AMAs, where nearly all the Type II rights are concentrated. Most transfers of Type II rights have been part of real estate transactions involving land and improvements as well as water, and little can be inferred about the implicit market value of water rights in these sales. A few Type II rights have been acquired separately by individuals seeking to invest in water rights.¹⁷ Some businesses have acquired Type II rights believing them to be cheaper means of getting water than hooking up to a municipal water system.¹⁸ In 1985 and 1986, typical prices for Type II rights averaged \$1,500 per acre-foot in the Phoenix AMA, and slightly over \$1,000 per acre-foot in the Tucson AMA.

An emerging market for Type I and Type II water rights is the leasing of water in order to open new water service areas. Under Arizona law, the service area for a water service organization is not necessarily the same as the area within which it has the legal authority to provide service. The former consists of the area physically served with water. The latter is little more than a boundary line on a piece of paper, including the current water delivery area but conceivably extending far beyond it. Water service organizations can only withdraw groundwater from areas already within their current service areas. It is difficult for a water service organization, especially a new one, to provide new water service without already having the water resources on hand. A possible solution is to lease water rights just long enough to establish water service, and then to apply to the State for a service area groundwater extraction permit.¹⁹

Surface water rights are also being transferred in Arizona. In the spring of 1984 the city of Scottsdale purchased the Planet Ranch, an 8,400-acre ranch in western Arizona for \$12.2 million. The source of water for the Planet Ranch is the Bill Williams River. Scottsdale hopes to divert water from the Bill Williams into the CAP aqueduct for transportation to the city.

Scottsdale has invested close to another \$4 million in improving the ranch facilities and preparing land for irrigation. Ranch operating losses over the next few years are projected to total \$1.5 million; the city expects to break even on operating costs in 1987.²⁰ Adjusting for inflation, the present value of the costs associated with acquiring the Planet Ranch water rights equals about \$17.7 million. If the ranch does in fact yield 13,500 acre-feet of water as hoped, the cost for the water will be approximately \$1,300 per acre-foot.

Inasmuch as the water rights for the Planet Ranch are appropriated rights and are subject to forfeiture if they are not put to beneficial use, Scottsdale will have to continue using them for agricultural purposes until they can be incorporated into the city's municipal water system. The precise quantity of water rights acquired in the purchase of the Planet Ranch and the proportion of those rights that may be removed from the river for transport

to Scottsdale have not yet been determined, although estimates place the quantity available for export at about 13,500 acre-feet per year. Aware of this uncertainty, Scottsdale included a clause in the purchase contract specifying adjustments in the ultimate sales price for the ranch should the water rights prove to be less than originally estimated.²⁰ If the water resources turn out to be less than expected quantity, the purchase agreement calls for a reduction in the sales price by \$870 for each acre-foot of water less than 13,500.

Other recent acquisitions of land and water rights in western Arizona include the Lincoln Ranch and the Crowder-Weiser Ranches, purchased by private real estate developers, and farms in the McMullen Valley, purchased by the City of Phoenix. The 1,000-acre Lincoln Ranch, located along the Bill Williams River upstream from Scottsdale's Planet Ranch, was purchased for approximately \$5 million. The owner hopes to transfer between 7,000 and 7,500 acre-feet of water per year to the Phoenix area. Informal discussions have been carried out with the City of Scottsdale about sharing in the cost of building a canal from the Bill Williams River to the CAP aqueduct.²¹

The Crowder-Weiser Ranch, located near Vicksburg in La Paz County, is expected to yield over 51,000 acre feet per year. Crowder-Weiser was acquired in a series of transactions in 1985, at costs ranging from \$500 to over \$900 per acre-foot for the water rights. A minority interest in the Ranch subsequently was sold to a third party for about \$1,200 per acre-foot. The water, which the developer hopes to deliver via the CAP aqueduct, will be used for projects in the Phoenix area.

In 1986 the City of Phoenix purchased 14,000 acres of farmland in the McMullen Valley in La Paz county for slightly over \$30 million. The city expects to export up to 30,000 acre-feet of water annually from the land by the year 2005. Phoenix is hoping to use the CAP aqueduct to transport its water from the McMullen Valley to its service area.²²

Sales of treated sewage effluent have occurred throughout central and southern Arizona. Pima County, in the Tucson AMA, has been selling up to 3,500 acre-feet per year of secondary treated sewage effluent to farmers in the Cortaro-Marana Irrigation District for several years at \$5 per acre-foot. Recently the district agreed to an increase in the rental rate to \$10 per acre foot. Tucson city policy now encourages all large commercial water users to purchase and use effluent to the greatest extent possible.²³ New golf courses are required to irrigate with effluent. Effluent charges for commercial water users in Tucson in 1986 were \$372 per acre-foot.²⁴

Another example of sewage effluent marketing is an agreement signed in 1973 between the Palo Verde nuclear power station and the cities of Tempe, Phoenix, Mesa, Tolleson, Scottsdale, and Youngtown—all in the Phoenix metropolitan area. The contract includes four separate purchase options, and if all are exercised, they would provide 140,000 acre-feet of effluent annually to cool the plant's reactors through the year 2040. The original price for the effluent was set at \$30 per acre-foot, or 40% of municipal users' cost of CAP water,

whichever is lower. A recent law suit challenging the agreement may force the contract to be revised.¹² If it is amended, the contracted price for the effluent could be increased to equal the cost of CAP water for cities, which now is expected to be at least \$300 per acre-foot.²⁵

To summarize, groundwater, surface water and effluent are being transferred through market transactions in Arizona. State laws that define and restrict water market opportunities vary considerably, depending on the type of water right under consideration. Water is steadily moving from irrigated agriculture to nonagricultural uses, and this trend will continue as rapid population growth continues in metropolitan areas.

SOUTHERN CALIFORNIA

Description of the Study Area

In California, as in many other Western states, water resources are concentrated in one part of the State while population, industry, and irrigated land is concentrated in another part of the State. Approximately 70% of the State's water supplies lie north of the latitude of Sacramento, while 80% of the State's population, along with most irrigated agriculture and industry, lies south of that latitude.^{26, 27} A complex system of dams, reservoirs, and canals transports water south through California's San Joaquin Valley. The federal Central Valley Project (CVP), which began deliveries in 1951, extends to the southern end of the San Joaquin Valley. California appropriated funds for the State Water Project (SWP) in 1959, and the SWP's California Aqueduct transports water south through the San Joaquin Valley, over the Tehachapi Mountain range, and into the greater Los Angeles Metropolitan Area. Features of California's water infrastructure are shown in figure 3.

Southern California, defined as the region south of the Tehachapi Mountains, is characterized by a semiarid climate and a large concentrated population. Southern California has over 50% of the State's population and contains the nation's third largest metropolitan area, yet receives less than 3% of the State's surface water runoff. The southern part of the State imports more water than it produces locally.²⁸ The southern California water industry is dominated by public districts and municipal waterworks. The Metropolitan Water District (MWD) of Southern California services more than half the water users in the region. Over fifty reservoirs operate in southern California, managed by federal, state, city, and other water agencies. Irrigated agriculture continues to be an important part of southern California's economy, in spite of rapid urbanization of agricultural areas. Agriculture uses approximately 60% of the region's water supplies, and urban areas account for the other 40% of water use.²⁹

Water Laws and Institutions

Approximately 55% of California's water supply is direct and stored surface water. Both riparian and ap-

propriated water rights are recognized under state law. While large quantities of water are used under riparian law, most of the surface water within the State is appropriated. Under an appropriative right, the user may divert allotted quantities of water from a particular source and location for a specific use, during a specific part of the year. Since 1914, appropriative rights have been created under a license system operated by the state. Appropriative rights are sometimes held by individuals or corporation, but they are much more commonly held by public entities organized for the purpose of supplying water such as the federal Central Valley Project (CVP), the California State Water Project (SWP), and local water districts. Agencies must obtain appropriative water rights before surface water development may be undertaken.³⁰

Groundwater rights in California are typically associated with land ownership. Owners of land overlying a groundwater basin are entitled to pump water desired for use on that land. This is known as "overlying use." If the basin has water in excess of demand, that excess may be transported for use on nonoverlying land. The difference between current groundwater pumping and an aquifer's "safe yield" (the average annual recharge of the groundwater basin) determines whether that aquifer's groundwater may be used on nonoverlying sites. There are no statewide groundwater basin management statutes. Court decisions have evolved the principle that groundwater overdraft can be reduced by mandatory limitations on pumping by each overlying owner, through a doctrine known as "mutual prescription."³¹

The California Department of Water Resources (DWR) was created by statute in 1956 to take the responsibility for all matters pertaining to water and dams. In 1967, the legislature merged the functions of the State Water Rights Board and the State Water Quality Control Board into the State Water Resources Control Board (SWRCB), which has jurisdiction over the nine regional water quality control boards. The SWRCB focuses on three distinct areas—water quality, water rights, and planning and research. The board has grown in stature and authority along with the growing concern for environmental issues in the State. The board acts in a quasi-judicial role in determining rights to surface water. Of particular concern to the board when making water rights determinations is the prevention of waste and unreasonable use of water.

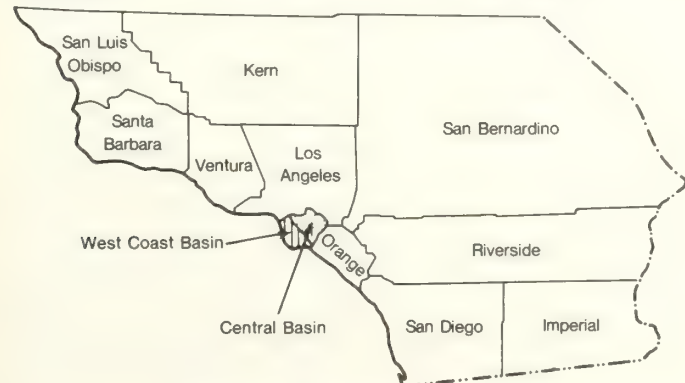


Figure 3.—Southern California.

California's water is allocated to its user, for the most part, through a hierarchy of government agencies. California water supply agencies are characterized by a wide diversity of scale and a variety of legal forms. Long-standing commercial water companies and mutual water agencies number in the hundreds. Their principal purposes are to establish rights to water use and to sell and deliver water to users. Mutual agencies sell water to members at supply costs and are thus nonprofit. Water companies sell water to customers within their service area at whatever prices the market will bear, and the profits are distributed to stockholders as with any other private company. It is not known how much water is allocated by these private entities, but mutual companies are more frequently utilized in irrigation, whereas commercial companies are more heavily involved in serving urban customers.

A wide array of private and public institutions exist for the purpose of developing and allocating water resources, employing operating rules established by enabling legislation. These rules largely determine the distribution of economic rents connected with water use and influence the efficiency of water development and allocation. More than 3,000 different organizations supply water in the State, of which nearly 1,000 are public water districts. About 900 of these public districts were formed under 40 general water district acts; the remainder were individually created by the Legislature by special acts.³²

The public water districts that supply most of the water to agriculture are reclamation districts, irrigation districts, and water districts. Their primary purposes are to reclaim and protect lands from overflow and to irrigate lands. These public districts are, in essence, nonprofit wholesalers of water. They may have water supply sources of their own, both surface water and groundwater, or they may contract for water developed by the federal government (the Central Valley Project) or by the State of California (the State Water Project). They are governed by boards of directors, may have powers of eminent domain, and have the power to sell general obligation bonds, levy water charges, and impose ad valorem taxes on landowners within the district. Most water service agencies function under appropriative water rights laws. Riparian users are typically small, and take water only for their own use.

The agencies and individuals participating in the water allocation system in California can be stratified into four levels. First are the courts and the State Water Resources Control Board; next are the federal and state water supply agencies; then come the regional and local water agencies. Water users comprise the lowest level of the hierarchy, but in many instances they are the holders of water rights. While much of the developed water initially was allocated through the federal and state water projects, some goes directly to regional and local water districts, and some goes directly to users.²⁸

Uncertainty over transferability of water rights makes water users reluctant to consider selling or leasing their water rights. Until recently, one of the biggest legal impediments to water transfers has been the "beneficial use" doctrine, which limits all water rights to an amount

“reasonably required for . . . [a] beneficial use.” While originally enacted as part of the California constitution of 1928 in an attempt to discourage the wasteful use of water, this doctrine actually inhibited voluntary reallocation of existing allotments to parties who could make better use of the water.³⁰ In 1982, the state legislature took steps to clear this legal obstacle to transfer by enacting a law permitting the sale or lease of water deemed “surplus” to a user’s needs.³³

In California, riparian surface water use and overlying groundwater use are legally defined on the basis of land ownership—the rights to use such water cannot be transferred independent of the land title itself. Hence, purchasing a piece of land with either riparian or overlying groundwater rights is akin to purchasing the land plus an option to use water on that land subject to its availability, to requirements for reasonable and beneficial use, and other restrictions discussed earlier.

The state Water Code, as amended in 1971, prohibits districts from transferring water to outsiders unless it is declared “surplus.” The test of “surplus” is strict and can rarely be met, apparently requiring the water to be unusable, at any price, by any member of the district. The enabling acts of many water districts do not provide for reallocation of water from one member to another once an initial allocation is made. Furthermore, as a general rule, riparian rights cannot be transferred for use on nonriparian land.

Appropriative rights are legally transferable, and can be sold, independent of title to land. They are the easiest water rights to transfer because the water right is recorded and the legislature has established procedures for transferring appropriative rights. The transferer must comply with the applicable provisions of water law governing a change in the purpose of use, place of use, and point of diversion. The Water Board may approve a transfer if it is in the public interest and there is no injury to other water users. In instances where the possibility for injury to other users is unknown, the board may authorize a trial transfer not to exceed one year in order to judge the effect of the transfer. The board may modify or revoke the trial transfer if it determines that the transfer will result in substantial injury to any water user. However, the occasions on which transfers actually occur are limited and always subject to the uncertainty of SWRCB approval. Appropriative groundwater rights are relatively uncontrolled, except when a groundwater basin becomes overdrawn, at which time overlying groundwater users have priority, and appropriative groundwater rights can become worthless.

Groundwater in adjudicated groundwater basins may be transferred only after a determination of the amount needed for reasonable beneficial use on overlying lands reveals that a surplus exists. The surplus may be appropriated for export. Surplus waters cannot be exported from the area if this will result in injury to other overlying owners.

Water Market Activity

The current system for defining and managing water rights in California presents obstacles to market allocation

of water. Individual water users often do not own the water rights themselves—the water companies or districts do. In California, the Bureau of Reclamation and the Department of Water Resources are permittees of the State Water Resources Control Board, which has ultimate jurisdiction over water rights. Contractors of these agencies technically do not hold any permanent water rights beyond their contracts. They are given options to purchase water from the districts on terms specified in the contract. The district, which is bound by contract to supply water, isn’t free to negotiate the sales of water rights or even water rentals unless it has surplus water available. In the case of State Water Project water, any changes in contracts or in points of diversion must be approved by the director of the Department of Water Resources. This type of administrative approval is likely to be difficult to obtain. The ultimate water users are powerless to make any transfers at all. The most they can do is simply forfeit their use of water, but usually they are committed by contract to take a certain amount. The result is an inflexible and inefficient water allocation system.

Options to buy State Water Project water are generally not transactable. They cannot be bought, sold, or leased without approval of the SWP. A series of water transfers took place within California during the 1976–77 drought, all under special circumstances. Nearly all of the transfers occurred outside of the SWRCB appropriations system, and with few exceptions, the water was sold by individuals or corporations with clear title to the water rights, rather than by a water district. These sales tended to be short-term leases negotiated in response to drought conditions.³²

Many of the transfers that occurred were within the Bureau of Reclamation’s Central Valley Project. The Emergency Drought Act of 1977 granted the Secretary of the Interior the authority to establish a temporary water program for the purpose of minimizing agricultural losses resulting from the drought. During the program’s period the Bureau purchased 46,438 acre-feet of water at prices ranging between \$20 and \$87 per acre-foot. The Bureau resold 42,533 acre-feet of water to various buyers at a price of \$53 an acre-foot plus conveyance charges.³⁴

The Bureau administratively determined the purchase and sales prices of the water. Under the act the purchase price could “not confer any undue benefit or profit to any person or persons compared to what should have been realized if the water had been used in the normal irrigation of crops adapted to the area.” The Bureau negotiated the purchase price by considering the seller’s net income adjusted by certain handling costs. Resale prices were restricted to cover the actual expenditure involved in acquiring and redistributing the water. Thus, the program rationed water allocation through a buyer preference system and marketed water simply at cost.³⁴

Water exchanges and transfers take place routinely in Central and West Coast Basins of Los Angeles County. These basins were adjudicated in the early 1960s and groundwater use is administered by the Department of Water Resources, which serves as court-appointed

Watermaster. Both basins participate in groundwater replenishment programs, sea water barrier projects, and water quality and groundwater level monitoring. The Watermaster administers an Exchange Pool, which facilitates transfer of water from water users who will not use their entire allotment to water users who desire water in excess of their current allotment. The price charged for Exchange Pool rights is based on a formula specified in the adjudication court orders, not on negotiation between water users. In 1985 the Exchange Pool price was \$184.29 per acre-foot in the Central Basin and \$69.54 in the West Coast Basin.³⁵

The Exchange Pool is not the only method of obtaining additional pumping rights. Water users may freely buy, sell, and lease groundwater rights within each basin. In the Central Basin, water rights sales over the past two decades have served to concentrate groundwater rights ownership, reducing rights holders from 508 in 1966 to 194 in 1985. Sales and leases are recorded with the Watermaster. Summary price information shows a steady rise in average leasing prices from \$50 to more than \$90 per acre-foot over the period 1964 to 1985. Privately negotiated leasing rates lie 20% to 30% below the Exchange Pool rates and are up to 50% less than Metropolitan Water District's rates per acre-foot. Pumping rights are viewed as a commodity in Los Angeles County. Pumping rights, including leases, are taxed as property rights by the County.³⁵

Wahl and Davis³⁶ note that substantial economic incentives exist for water transfers between the federal CVP and the SWP, both of which move water south through California's San Joaquin Valley. In particular they argue that farmers in the Westlands Water District, who are confronted with the water quality impacts of agricultural drainage on Kesterson Reservoir, would be willing to sell land and water rights to the State Water Project for prices that lie below the costs of SWP's least expensive supply development alternatives. While clear economic incentives for the transfer exist, the author points out that unresolved legal questions remain a barrier to CVP-SWP transfers, as do the high transaction costs of multi-agency cooperation and negotiation.

Southern California's Metropolitan Water District has been engaging in complex negotiations with Imperial Irrigation District (IID) for transfer of conserved water for IID to MWD. MWD proposes to finance conservation measures within IID in exchange for rights to use conserved water. The average cost per acre-foot for 400,000 acre-feet of conservation investments is \$240 per acre-foot conserved. This represents an economically attractive source of water, relative to MWD's other supply enhancement alternatives. However, negotiations have proved complicated because of legal uncertainties, federal and state agency concerns over the proposal, and MWD and IID concerns over security of rights transferred and terms of transfer.³⁶

MWD is also investigating the possibility of receiving federal CVP water in drought years in return for MWD assistance in constructing distribution systems for a San Joaquin Valley Water District and for MWD provision of SWP water to that district during wet years. This proposal is in the early stages of negotiation.³⁷

There is increasing pressure in California to permit development of water markets. It is the established policy of the State of California to encourage the voluntary transfer of water and water rights. The legislature has specifically stated that transfer of water or water rights does not, in itself, constitute evidence of waste or unreasonable use. Recent California legislation permits water to be transferred if the water use has been reduced or discontinued because of the substitute use of reclaimed or waste water. Additionally, the law now permits the transfer of appropriated water and an appropriative water right if the use has been discontinued or reduced because of water conservation efforts. These transfers must be undertaken pursuant to the provisions of laws governing transfers. Under other legislation passed in 1982, any regional or local public agency authorized to serve water may not transfer surplus appropriated water to users outside its boundaries. Any appropriated water may be transferred if the agency and individual water users and right holders agree. Given these developments market transfers of water in California are likely to become increasingly common.

NORTHEASTERN AND SOUTHEASTERN COLORADO

Description of the Study Area

The market areas chosen for study in Colorado are the Northern Colorado Water Conservancy District (NCWCD) and the Southeastern Colorado Water Conservancy District (SCWCD). The NCWCD includes irrigated and dryland farming areas, town, and cities in the South Platte River basin. The principal metropolitan centers included in the district are the cities of Boulder, Fort Collins, Greeley, Longmont, and Loveland. The SCWCD includes irrigated and dryland farming areas, towns, and cities in the Arkansas River basin. The principal metropolitan centers included in the district are the cities of Pueblo, Fountain, and Colorado Springs. Another city located outside the SCWCD in the Denver area, Aurora, has successfully transferred water out of the Arkansas basin and is currently attempting to purchase and transfer additional water rights out of the basin. Aurora is therefore included in the discussion of SCWCD water transfers. The areas are shown in figure 4.

The predominant source of water in both market areas is mountain stream runoff. The natural supply of surface water is supplemented with transmountain diversion projects and with groundwater pumping during periods of peak demand. Transmountain diversion water and most native stream water are of high quality, except for flows in the lower reaches of the Arkansas where salinity levels are significant.³⁸ Groundwater quality varies depending on location, but is generally poorer than that of surface flows.

Nearly all native water supplies appropriated for use below (east of) the front range of the Rocky Mountains are controlled by mutual stock irrigation companies, privately held irrigation companies, rural-domestic water districts, or municipal water service organizations. Some

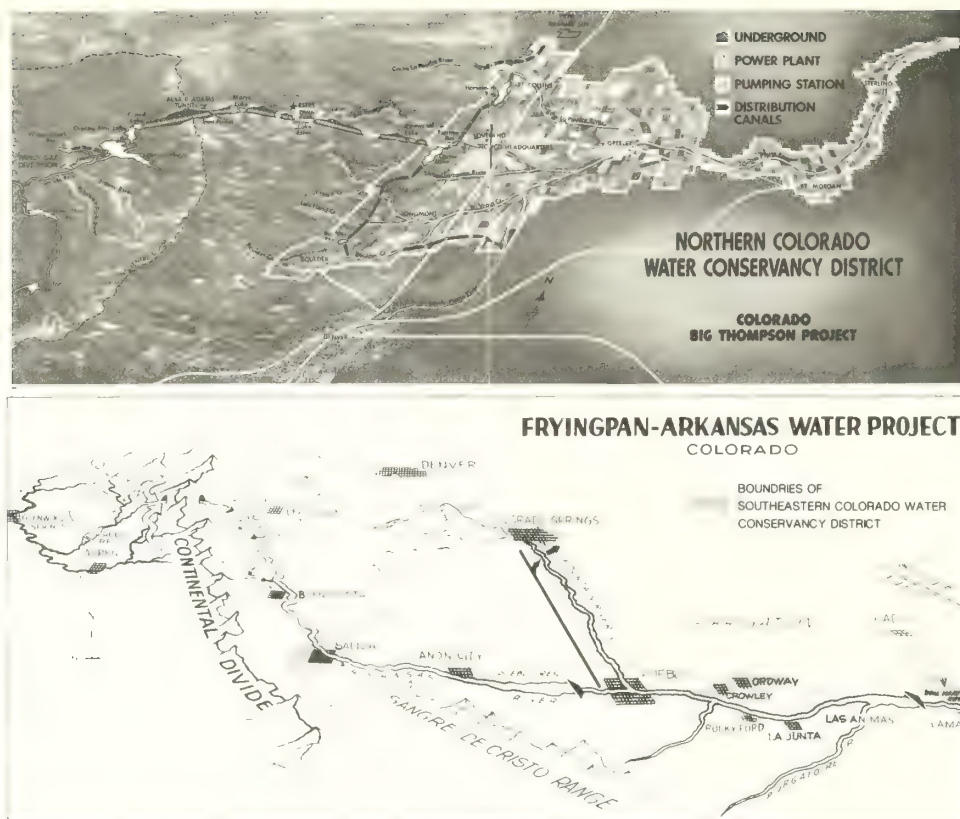


Figure 4.—Northeastern and Southeastern Colorado.

native water mapflows, especially in the upper reaches of the Arkansas River, are still held under individual appropriation decrees.

There are two major transmountain diversion projects in the NCWCD, the Colorado-Big Thompson Project (C-BT) and the Windy Gap Project. The C-BT was the first and largest transmountain diversion project in Colorado. Built by the Bureau of Reclamation in the late 1950s, the C-BT delivers up to 310,000 acre-feet of water per year to agricultural and municipal and industrial users throughout its service area.³⁹ The locally financed and newly completed Windy Gap Project, which began deliveries in 1985, promises to furnish primary rights to an additional 48,000 acre-feet of water for municipal and industrial users in the area. Return flows from the Windy Gap Project will be transferred to other water using entities for a variety of purposes including irrigation, domestic use, and groundwater recharge.⁴⁰

More than a dozen transmountain diversion projects have been constructed to serve the Arkansas River basin, although none approaches the size of the C-BT. Most of the projects are owned in their entirety by individual municipal water service organizations. The two major exceptions are the Twin Lakes and Frying Pan-Arkansas (Fry-Ark) Projects, which were constructed by the Bureau of Reclamation. The Fry-Ark Project, managed by the Southeastern Colorado Water Conservancy District, is the largest transmountain diversion works in the Arkansas River basin. The Fry-Ark delivers approximately 80,000 acre-feet of water to agricultural, municipal, and industrial users in the SCWCD. About 70% of the water comes from transmountain diversion,

while the remaining 30% is developed from “storable flood waters” of the Arkansas River and its tributaries.⁴¹

The Twin Lakes Project is an enlargement of the old Twin Lakes Reservoir and Canal Company system, which originally handled only native flow waters but is now primarily a transmountain diversion project. The system is partly owned by the Federal Government and partly by the Twin Lakes Reservoir and Canal Company. The shares of mutual stock that may be bought and sold on the market represent only that portion of the water in the reservoir controlled by the private water company. All remaining storage space in the reservoir is used to support the Frying Pan-Arkansas project. Roughly 10% of the total average annual yield of Twin Lakes stock is attributed to native flow while the rest represents transmountain diversion water rights deeded to the company by the Bureau of Reclamation.⁴² About 50,000 acre-feet of water per year are delivered to Twin Lakes company stockholders. Originally all of the water was controlled by irrigators, but now the company is almost completely owned by the cities of Aurora, Colorado Springs, Pueblo, and Pueblo West.⁴³

The water service infrastructure within the NCWCD is much more integrated and extensive than that within the SCWCD. The system of capturing, storing, and distributing water resources in the NCWCD constitutes one of the most complex and flexible water supply networks in the Western United States. Dozens of different water service organizations operate hundreds of miles of canals, storage, reservoirs, pumping facilities, and water treatment plants serving an area roughly equal in

size to the State of Connecticut. Conditions are much different in the Arkansas River basin. Whereas population, water resources, and economic activity are distributed throughout the upper South Platte basin, they are relatively concentrated in the Arkansas basin along the base of the front range, in the Fountain Valley (a tributary to the Arkansas) and along the narrow band of the Arkansas River itself. Water storage and delivery facilities are less developed, and the opportunities for exchanging water among different organizations are correspondingly less.

Irrigated agriculture is the predominant water user in both market areas. However, rapid urban expansion in every metropolitan center throughout the NCWCD has caused irrigated land to be retired and developed. Growth has brought pressure to transfer water rights out of irrigation to municipal uses. The process has been gradual and continuous in the NCWCD, while it has been uneven and sometimes abortive in the SCWCD.

The geographical locations of water resources, population centers, and economic activity in each of the two areas have had a strong influence over the nature of the water markets. In the NCWCD, the newer nonagricultural water users are intermingled with older agricultural users. Expanding urban developments often acquire additional water rights by expanding onto previously irrigated farmland. Hence, urban development tends to replace irrigated agriculture in the NCWCD in a smooth and orderly transition.

In contrast to the relatively unencumbered transfers of water rights experienced in the Platte River basin, transfers in the Arkansas River basin have been complex and difficult. The main centers of population growth and new economic activity in the SCWCD are clustered about the centers of Pueblo, Colorado Springs, and Fountain (and Aurora), which are located upstream from most existing water users. Transferring water rights from the old water users to the new ones does not involve a simple change of use within the same general area. Water rights must instead be transferred over long geographical distances and across jurisdictional boundaries. Conflicts over water transfers are common. New water development projects in recent years have provided costly but practical alternatives to the uncertainties and difficulties involved in water rights transfers.

Water Laws and Institutions

Water rights in Colorado have been subject to the legal doctrine of prior appropriation since statehood was declared in 1876. All groundwater and surface water rights must be put to beneficial use or risk forfeiture.⁴⁴

Surface Water Rights

Surface water rights in Colorado are of two different types—streamflow and reservoir rights. Appropriated stream flows are generally quantified in terms of flow rates and priority dates. Appropriators may withdraw water from the stream at specified maximum flow rates

(cubic feet per second) so long as the flow rate in the stream itself is at or above some specified minimum level. The more recent the priority date, the higher is the minimum streamflow rate required to activate the right. In contrast, reservoir rights are specified in terms of acre-feet of volume. During any given year the most senior reservoir right holders may fill their reservoir(s) to the capacity of their right first, followed by the next most senior right. Reservoir rights are usually activated in periods of high streamflow (winter and spring runoff) before the beginning of the irrigation season.⁴⁵

Reservoir rights in Colorado are extremely important. Most stream systems in Colorado are highly variable, alternating between periods of flood and drought. Without a means of regulating water supplies, appropriators in Colorado could not expect to have reasonably secure water supplies unless they held very senior water right and/or a quantity of rights disproportionate to their average use patterns. Storage facilities can also increase the effective volume and thereby the value of a water right. They allow users to regulate the timing and volume of releases to conform to their patterns of use with minimal waste. Supply fluctuations can be smoothed out and waste minimized by storing unused water during periods of high water flow and releasing them for use when natural water flows are low.

Another important advantage of having access to water storage facilities in Colorado is that they facilitate water exchanges—one important means of optimizing the use of water resources and water rights that are unevenly distributed over time and space among two or more water users. A good example of a water exchange that necessitates the use of reservoir space is an arrangement the city of Colorado Springs has recently developed and which is still pending final approval in water court. Historically, Colorado Springs had released its treated effluent into the Fountain River, where it provided a windfall gain to downstream appropriators in the Fountain and Arkansas River systems. Now the city exchanges a portion of its return flow with a compensating quantity of water in Pueblo Reservoir (located upstream from the confluence of the Fountain and Arkansas Rivers), and then exchanges this water further upstream for its mountain reservoirs. From these reservoirs Colorado Springs is able to draw the water to the city through its existing conveyance system. Although there have been protests from downstream appropriators who claim that Colorado Springs forfeited the right to recapture its return flows after years of nonuse, the city is confident that eventually its right to the exchange will be affirmed.

Water rights transfers in Colorado are often complicated by the fact that both flow rights and storage rights may change hands in a transaction. Because of the flexible nature of storage rights, their market value may reflect far more than the value of the water that could be impounded in a single filling of the right. It is not unusual for a buyer to acquire a package of water rights primarily for the purpose of gaining additional storage capacity and only incidentally to increase its inventory of water rights.

Storage rights may increase the value and usefulness of several different water rights through allowing the rights holder to capture, store, and/or exchange quantities of water several times over the course of a single season. The storage right itself is valid for only a single filling of a reservoir per year. Once the water right is used, however, the storage space may still be available for other purposes. Users may refill their space in a reservoir with exchange water or stored water that they have under other flow decrees. Tourquoise, Spinney Mountain, and Twin Lakes reservoirs all serve this latter purpose for the cities of Colorado Springs and Aurora. The storage space available in these reservoirs form essential links in bringing water from many scattered flow rights into the cities.

Groundwater Rights

The application of the appropriation doctrine to groundwater rights has been a slow and uncertain process. The classic distinction made in most states between “percolating” groundwaters and those in “definite streams or channels” has not been important. Distinctions of greater legal significance are found between groundwaters that are tributary to a surface watercourse and those that are not. Little legislative action is found concerning groundwater in the early history of Colorado because groundwater supplies were not extensively developed until fairly recently. For most of the State’s history, groundwater wells have been allowed to develop as if they took water from a source of supply entirely separate from the surface water streams. It was inevitable that as more and more groundwater resources were developed, the effects would begin to be felt on surface water flows.⁴⁶

Since most existing groundwater appropriations are junior to most surface water appropriations in use, both the Arkansas and Platte River basins are now closed to additional groundwater appropriation. Those groundwater resources that are judged to be tributary to a surface water flow are limited in the number of days of the month that they can operate. If groundwater users wish to pump beyond the legal limit, they are required to file an approved “augmentation plan” with the State. Alternative means of augmenting stream flows affected by groundwater pumping include acquiring and then retiring stream flow rights, releasing stored water into streams, or purchasing another water user’s return flow for release into streams.⁴⁷

Appropriation decrees for water rights in Colorado provide no volumetric limitation on the extent of a right. State law prohibits the wasteful use of water, but does not specify what constitutes waste. For land to be irrigated in Colorado, it must either have an original appropriation of water rights appurtenant to the land, or have existing water rights transferred to the land, or be included within the service area of a water company that supplies irrigation water. Irrigation water rights may be supplemented by renting additional water for any length of time desired.⁴⁷

Under Colorado law, the appropriative right to water is a property right separate from the land to which the

right is appurtenant. Hence, the land for which a water right was appropriated or the water right itself may be transferred in part or in its entirety independent of one another. Water rights may be freely bought, sold, or rented as a general rule. However, if the transfer of a water right involves anything more than a change in ownership, the state must ensure that no other existing water rights users will suffer injury. If the only change in a water right is a change in ownership, there is no limitation on the right to transfer and no approval is required by the State. Conveyance of a water right separate from the land, however, or any proposed change in the point of diversion or place or purpose of use, is monitored strictly to protect the rights of all junior and senior appropriators on the particular stream system.⁴⁸

The state Supreme Court appoints a Water Judge for each of the seven administrative water districts in Colorado. In the judicial process in Colorado, the district water courts play the primary role in determining water appropriations, and the merits of an anticipated transfer of water rights. Colorado law specifies that to make a change in point of diversion or place or purpose of use of a water right one must bring suit in a district water court. The purpose of this litigation is to allow the court to hear all protests to the transfer so that no person with alleged property rights in the area affected by the water transfer will be injuriously affected. Change applications are generally approved if it can be demonstrated to the satisfaction of the Water Judge that the change will not adversely impact third parties. Changes might still be allowed in the face of third-party effects if the presumed injuries can be appropriately mitigated or compensated.

Water rights transfers are often difficult in Colorado. The major problem is the uncertainty with regard to how the water rights will be quantitatively defined by the courts. Courts must consider multiple users of water associated with a given set of appropriations and related return flow patterns. Return flows give rise to subsequent sets of secondary appropriations that vary with the availability of water as determined by return flow, storage facilities, groundwater sources, precipitation, and other factors.⁴⁹ Furthermore, there are no predetermined measures of consumptive water use for specific economic activities or by geographical locations. The water court must decide on an ad hoc basis the net impact on a stream system of a particular appropriation, and then deduce from available information the average consumptive use of water from this appropriation. Generally, it is the consumptive use portion of the water right (i.e., the net quantity of water historically removed from the system under the existing appropriation) that is judged by the water court to be the quantity transferable to a new location and use.

Water rights transfers are further complicated by the adversarial nature of water court proceedings. Since the State Engineer is not consulted on proposed water rights transfers, the courts call for engineering reports from each of the contesting parties. Both the petitioners for the water rights transfer and the protestants are called upon to support their contentions relating to the transfer. The court must make a choice or a compromise between conflicting testimonies, without the benefit of unbiased

and objective professional engineering skills and information.

In spite of these obstacles, water transfers are common in Colorado, primarily owing to the existence of a number of institutions, statutes and water court rulings that can simplify the water transfer process by reducing or eliminating the legal claims of opposing parties. For instance, water in one hydrologic basin may be appropriated and “exported” or transferred for use in other hydrologic basins. Once the transbasin diversion of water is accomplished, users of “imported” or “foreign” water do not have the return flow obligations that users of “native” flows have to other appropriators in the same area. Holders of imported water rights may transfer their water rights to any user within the decreed area of use for the water right without liability. Court proceedings are necessary only if an owner of transmountain water rights wishes to transfer water out of the original area of use, or use it for a purpose of use not specified in the appropriation decree.

Imported Water Rights

Holders of imported water rights have dominion over the entire right. They may use and reuse and/or sell the water to extinction (total consumption), so long as the water can be identified. Suppose, for example, that a water user owns 100 acre-feet of transmountain diversion water and can demonstrate to the satisfaction of the water court that 70% of the water it uses returns to the stream system. The user may then develop the right to reuse or sell the 70 acre-feet. Suppose it sells the 70 acre-feet of return flow rights to an irrigation company downstream, which in turn can demonstrate that 30% of its use is return flow. The company may therefore in turn either recapture 21 acre-feet or sell it to yet another water user, and so on until the water is either abandoned or totally consumed within the system.

District water courts in the areas of the NCWCD and SCWCD have handed down opinions that essentially give transferred native flow rights the same legal status regarding the returning return flows as imported waters. Because only the consumptive use portion of a native flow right is transferred, and that portion is by definition the quantity of water historically lost to the system, it may be presumed that no appropriators to native stream flows have any claim to the water. Rights to native flow waters that have already been transferred are therefore rights to the entire measure of the right, and may be used, reused, and/or sold to extinction. Although the implications of the rulings of these courts have not yet seen widespread application in Colorado, they may have a significant impact on the future transfer and management of water rights.⁴²

Water Companies

Water companies typically control a “bundle” of different water rights, including decreed native flow rights, reservoir rights, and transmountain diversion water.⁵⁰

The significance of company ownership of water rights is that the water is appurtenant to the company’s service area as a whole and not to any specific parcel of land. All water rights managed within the company service area are legally recognized as having the same point or points of diversion (the company diversion works) and the same place of use (the company service area).

Individual water users in the company service area own a proportional interest in the company, most often represented by shares of stock. Dividends in the form of water allotments are declared on the basis of stock ownership rather than on land ownership. The size of the allotment varies from season to season in accordance with the hydrologic cycles of the system, but the long-term average yield and the variability of water service per share of stock generally is well known. The water stock, and the water service represented by that stock, is legally considered personal property that can be bought, sold, or rented for any desired length of time within the company service area, without the need for proceedings before the district water court. Transfers of water company stock require proceedings before the water courts under only two circumstances—if the contemplated transfer includes a change in the purpose of use or if the stockholder wished to transfer water outside the company service area.

Twin Lakes Reservoir and Canal Company water is marketed in the same fashion as any other mutual water stock. The only difference is that a small portion of the water rights held by the company are recognized as native flow rights, while the rest are transmountain diversion water rights. In the early 1970s the city of Aurora purchased some Twin Lakes stock, but secured a court decree to transfer only the transmountain portion of the water rights to the city, located in the South Platte basin. Before the city could transfer the native flow portion of its Twin Lakes water rights as well, the district water court would have to determine the transferable (consumptive use) portion of the native flow component of the water rights. The yield on Twin Lakes stock held by Aurora averages slightly less than the yield on other shares of Twin Lakes stock held by other parties who retain the stock within the South Platte basin and have access to both the transmountain and native flow portions of Twin Lakes water.⁴²

Public Project Water

Mechanisms and procedures for managing public project water can vary substantially within Colorado. The Fry-Ark and C-BT were both conceived as multipurpose projects to supply supplemental water to existing irrigated lands and growing urban centers. The means of allocating water under each project to its users, however, are very different.

Shortly after its creation in the late 1950s, the governing board of directors of the SCWCD decided that the allocation of Fry-Ark water would be fixed at 51% for municipal and industrial use and 49% for irrigation. The allocation may be changed by the board in the future to

reflect conversion of agricultural lands to nonagricultural use. Users of Fry-Ark water who transfer any or all of their other water rights to other users do not have the privilege of replacing these rights with Fry-Ark water.⁴¹

Each year the board makes a determination of how much water will be available for distribution to eligible project beneficiaries. It then contracts with each individual water user or water service organization in the conservancy district that wishes to buy the water. Nobody is required to buy project water. The unit price for Fry-Ark water is predetermined by the board and is the same for all users. The governing board of the SCWCD exercises dominion over both the first rights to Fry-Ark water and to its return flows. No user has the right to sell project water available for delivery in any given year. Return flows are sold by the SCWCD for the same price as primary use water (\$8 per acre-foot)⁵¹. They are available only to those individuals or water service organization who are eligible to purchase Fry-Ark water. Most return flows are purchased by groundwater users in the district to meet state requirements for groundwater augmentation.

The Fry-Ark system of water allocation offers water storage programs for its users in order to use their decreed flow rights more efficiently. Users are allowed to store any unused quantities of their Fry-Ark water in project storage facilities. Agricultural users may hold their unused water until May 1 of the following year, while municipal and industrial users may carry their unused water over from year to year.⁵¹ The carryover program is limited by project reservoir space. SCWCD also allows agricultural users to store their own (nonproject) decreed native flow rights during the winter season for use in the summer.⁵² Whereas decreed flow rights in other areas of Colorado sometimes specify a particular season of use for the right (typically April 1 to October 1), most direct flow rights in the Arkansas River basin are active all 12 months of the year. Large quantities of water that previously had to be released downstream unused may now be captured and stored in Pueblo Reservoir for later use. The District charges \$3.20 per acre-foot of water stored, and the water may be stored until May 1 of the following year. Under the Winter Storage Program several cities and towns that have storage rights in their own privately owned reservoirs may also retain their direct flow rights for use later.

The C-BT project differs in a number of important respects from the Fry-Ark. Water allocated under the C-BT project was deeded directly to the individuals and the water service organizations within the project service area who expressed an interest in participating. The NCWCD retains all rights to the return flows of project water, but each water user has the full right to purchase, sell, trade, or rent rights to the primary flows.⁵³ Return flows from the C-BT may be neither recaptured nor resold by C-BT users. Return flows that are not allocated by the NCWCD to its users simply remain in the river. The effect has been to firm up the water supply available under native flow appropriations on the lower reaches of the South Platte. Water users at the downstream end

of the NCWCD have found little advantage in holding on to shares in a project that effectively provides them with water whether they participate directly in the project or not. Most downstream appropriators have sold most, if not all of their C-BT rights to upstream users.⁵⁴ Unlike the Fry-Ark, the C-BT System does not allow carry-over or storage privileges.⁵³

The water rights to the C-BT are represented by 310,000 shares, or units. An annual fee to cover the fixed and operating costs of the project are assessed on each unit owned. The vast majority of C-BT units are held either by individuals for the purpose of irrigation, or by municipal or domestic water service organizations. A smaller number of miscellaneous units are held by collective irrigation organizations, nontaxable entities, and manufacturing concerns.⁵⁵ Generally the only restriction on the ownership of C-BT units by individuals is that the units must be assigned (appurtenant to) a parcel of irrigable land. The NCWCD discourages excessive speculation in C-BT water by limiting the ownership of project units to only that quantity that may be put to beneficial use on the property or within the service area to which it is assigned. As a hedge against future growth and also against supply fluctuations, municipal and rural water service organizations are permitted to hold rights in excess of current use.

The Windy Gap Project was planned, organized, and funded locally by the cities of Boulder, Estes Park, Fort Collins, Greeley, Longmont, and Loveland. Since the project's inception, Fort Collins has transferred its direct interest in the project to the Platte River Power Authority, and Estes Park has sold part of its interest to the city of Broomfield and to the Central Weld County Water District. Each participant in the Windy Gap Project assumes a proportionate share of the responsibility for the project costs, and in return has the right to a proportionate share of the water supply available for delivery through the project. Owners of Windy Gap water can use the primary flow and then reuse or sell the return flow to extinction, as long as it can be identified. The service area for the Windy Gap Project, that is, the area within which Windy Gap primary and return flow rights can be used and/or marketed, includes all of the NCWCD and some additional areas to the south.

Water Market Activity

Water markets in northeastern and southeastern Colorado differ greatly in both the frequency and nature of activity, and in the degree of access that the various users have to the market. In northeastern Colorado, willing buyers and sellers are often within the same water company service area, while those in southeastern Colorado usually are not. Users in northeastern Colorado usually can transfer water rights simply by signing a stock certificate, but in southeastern Colorado nearly any major transfer requires formal water court proceedings to change the point of diversion and place of use of the water rights to new locations.

Northeastern Colorado

Northeastern Colorado has a very favorable institutional environment for allowing the transfer of large quantities of water rights over wide geographical areas. The single largest source of water in the area, the C-BT, is also the easiest type of water to transfer. The only source of water in southeastern Colorado that has been marketed freely over a wide area, Twin Lakes, represents a small portion of the total available water resources available to users in the Arkansas basin. Furthermore, these water rights are now almost impossible to buy. When Twin Lakes stock came on the open market for nonirrigation use several years ago, almost all of it was purchased quickly by a few large users. Since then, virtually no shares of Twin Lakes stock have been offered on the market.

Although water rights transfers have been observed in northeastern Colorado for many years, the existing market began to assume its present characteristics with the completion of the C-BT project in the last 1950s. From the beginning, the project was intended to provide water to agriculture, private homes, and commercial businesses in varying proportions over time. In order to ease the transfer of water rights from irrigation to nonirrigation use, the appropriation decree permitting the transfer of water from the West to the East slope stipulated that C-BT water could be used for either irrigation or non-irrigation purposes. Municipal water service organizations and rural-domestic water companies have therefore been able to acquire C-BT units from irrigators without applying to the water courts for the right to change its point of diversion, place of use, or purpose of use. Moreover, they are free, wherever they choose, to rent any portion of their unused C-BT water back to irrigation users without obtaining special authorization.⁵⁶

When the 310,000 units of the Colorado-Big Thompson Project were distributed by the NCWCD to project participants in the 1950s, nearly 85% were assigned to agriculture. The remaining 15% assigned to other uses was adequate to meet virtually all nonagricultural demands for C-BT water and there was little pressure to reallocate supplies. Until about 1961, the market value of C-BT water was zero.⁵⁶ Purchase records of municipal water departments and rural-domestic water service organizations indicate that the market price for C-BT units became established in the early 1960s at a price of about \$95 per acre-foot. With each C-BT unit representing a long-term average yield of about 0.75 acre-feet, the average price of C-BT water was about \$125 per acre-foot. Through the 1960s and 1970s, prices for C-BT water climbed at an accelerating rate. Prices reached \$220 per acre-foot in 1963, \$560 by 1967, \$860 by 1971, over \$1,000 by 1974, over \$2,500 by 1977, and \$3,600 by 1980. After 1980, prices began to decline again rapidly. In 1981 prices fell to below \$3,000 per acre-foot, to less than \$1,600 by 1983, and to about \$1,000 by 1985.

Shares of stock in the North Poudre Irrigation Company are considered by many in northeastern Colorado to be the most marketable water rights in the NCWCD after the C-BT. The company's issue of 10,000 shares of

stock is held by a variety of municipal and industrial, rural-domestic, and agricultural water users within a service area covering much of the northern portion of the NCWCD. The long-term average yield on each share of stock is just under 6 acre-feet per year. Stockholders may split their shares up into quarter-shares representing an average yield of about 1.5 acre-feet per year in order to buy and sell smaller quantities of rights. There were 9,926 shares of stock outstanding (in general circulation) in 1984. A substantial portion of the water rights controlled by the company consist of senior direct flow rights, reservoir rights, and C-BT units.^{54, 57}

North Poudre water stock is an extremely marketable commodity similar to C-BT water rights in several ways. Both have large and reliable water supplies available to many different types of users, serve an extensive geographical area, have a large number of available shares, and allow small quantities of water to be transferred in a single transaction. Typical prices for North Poudre stock have followed the historical movement of C-BT prices. On an acre-foot basis, North Poudre water generally sells for between 60% and 70% of the going market price for C-BT units.⁵⁴

Comparable acre-foot quantities of other water rights within the NCWCD typically sell for 50%, 35%, or even less than 20% of the market value of C-BT water. These are water rights that tend to be less transferable. Some are available for use by only a relatively small number of potential buyers within a limited geographical area. Some provide water that is locked into agricultural use, and their transfer to a nonirrigation use would require potentially expensive legal proceedings. In addition, many of these alternative water supplies are either not reliable or are unavailable in a form useful to the buyer. Most of the adjudications for irrigation rights in northeastern Colorado restrict use to certain times of the year only. Many water rights cannot legally be used for more than a few months during the spring and summer. Municipal and rural-domestic water suppliers, whose customers demand steady supplies of water throughout the year, have a limited demand for highly seasonal water rights.⁵⁷ The less flexible ditch rights, privately adjudicated water rights, small private reservoirs, and groundwater rights are rarely sold apart from the land to which they are deeded. Most often these water rights are retained for agricultural use and their market values are low.⁵⁴

Windy Gap water has the potential to become one of the most flexible and marketable water resources in northeastern Colorado. Windy Gap is reputed by many to be one of the major reasons for the sudden turnaround in skyrocketing water rights prices during the early 1980s. Windy Gap has only recently been completed, however, and there are many uncertainties about its ultimate cost and usefulness. There are two main barriers to buying and selling primary rights to Windy Gap water at the present time—the high cost of participation in the project, and the system of ownership. Windy Gap is the most expensive source of primary water rights in northeastern Colorado. The current annual cost to project participants, including bond debt service and operation and maintenance costs, is between \$200 and \$300

per acre-foot. Participants in the project hold prorated shares of bonded indebtedness in proportion to their entitlement to the water. The sale of primary Windy Gap water necessitates the transfer of an equal share of the bonded indebtedness, which can be a very complex transaction.⁵⁴

Few transfers of the primary water rights in the Windy Gap Project have taken place thus far. The best examples are two sales by the town of Estes Park. In the summer of 1985, the town sold an interest in 100 acre-feet per year to the Central Weld County Water District for about \$510 per acre-foot. In the fall of 1985 Estes Park concluded another agreement to sell 3,700 acre-feet of primary Windy Gap rights to the city of Broomfield for about \$415 per acre-foot.⁵⁸

Interest in the Windy Gap Project remains high despite the cost of the water relative to the current market price for alternative water supplies in northeastern Colorado. Participants in the project believe the advantages of having Windy Gap water will prove to be worth the costs because they own not only rights to primary flows but also the return flows. They are free to recycle their shares of Windy Gap water by selling the return flow to a downstream user or by applying it to water exchanges or groundwater augmentation plans.⁵⁹ Since Windy Gap is operated jointly with the C-BT and they share a common service area (the service area for Windy Gap is actually larger than and includes the NCWCD), Windy Gap will share the same market area and have many of the same market advantages that C-BT water has.

Water rights purchased from agriculture by non-irrigation users are rented back to agriculture in large quantities every year. Municipal and rural-domestic water service organizations maintain large inventories of water rights in order to protect their users against fluctuations in supply. On the average, less than half of the C-BT units owned by nonagricultural water users are actually used. Since the NCWCD does not carry over unused water rights to subsequent years, shareholders have an incentive to at least cover the costs of assessing the units by renting the water to other users. Almost the only buyer for rental water in the district is irrigated agriculture, although in a few cases nonagricultural water service organization have also rented water.⁶⁰

The rental market for C-BT and other types of water rights in northeastern Colorado exhibits none of the price trends observed in the purchase and sales of rights. Prices have remained low, with no definite trend over time, varying between about \$5 and \$20 per acre-foot. With the development of the Windy Gap Project and with urbanization continuing in the NCWCD, it does not appear that rental water will become more scarce in the foreseeable future. More and more water rights have been acquired for development by municipal and rural-domestic organizations and offered for rent to agricultural users. Meanwhile, irrigated acreage continues to decrease and agricultural demand for water is declining. Even in relatively dry years and even at prices that are equal to or only slightly above the cost of the annual assessment costs for their water rights, renters frequently fail to find enough takers for all of their surplus water.

Southeastern Colorado

Activity in the southeastern Colorado water market is at once much simpler and more difficult to describe than the market in northeastern Colorado. Southeastern Colorado is simpler to describe because there has been much less market activity than in the NCWCD. However, most of the important water rights transfers have necessitated extensive negotiation and litigation over controversial issues and complex details.

More than a dozen different transmountain diversion projects bring some 200,000 acre-feet of water per year into the Arkansas River basin. Of all the transmountain diversions, however, only the 50,000 acre-feet of water provided through the Twin Lakes Reservoir and Canal Company have ever been marketed. Nearly all of the Twin Lakes stock came onto the market and was sold within a period of about 5 or 6 years in the 1970s.

The approximately 45,000 shares of outstanding stock in the Twin Lakes company were all originally owned by farmers within the service area of another irrigation water provider, the Colorado Canal Company, located about 50 miles east and downstream of the city of Pueblo along the Arkansas River. Two other water service organizations located in the same general area are the Henry and Meredith Reservoir Companies. These four irrigation companies provide three different types of water rights—transmountain diversion and some native flow water from Twin Lakes, native flow rights through the Colorado Canal, and reservoir rights from Henry and Meredith Lakes. Most farmers owned stock in all four water companies and had their water delivered to them through the Colorado Canal system.⁴³

Until about 1970, farmland in the Colorado Canal company service area sold for about \$500 per acre, including land and all water rights. In the early 1970s an investment group called the Crowley Land and Development Company (CLADCO) offered farmers in the area about \$900 per acre. Despite heated local opposition, farmers in the area sold a majority of their land and water company stock to CLADCO. As a result, slightly over 60% of the Twin Lakes stock changed hands. Nearly all of the remaining stockholders formed a coalition that became known as the Proxy Group.

CLADCO and the Proxy Group successfully obtained a decree in water court to change the purpose of use for Twin Lakes water rights from irrigation to multiple use.⁶⁰ The status of the other native flow and reservoir water rights appurtenant to lands in the Colorado Canal service area were not affected by this decision. Twin Lakes stock suddenly became one of the most flexible and valuable sources of water in the area, and nonagricultural users quickly bid up its price.

Between 1972 and 1975 CLADCO and the Proxy Group each sold large quantities of Twin Lakes water stock to the cities of Pueblo, Pueblo West, and Colorado Springs for prices ranging from about \$2,300 to \$2,400 per acre-foot. In 1976 another lot of Twin Lakes stock that had been transferred from CLADCO to the Aetna Group was sold in turn to the city of Colorado Springs for slightly over \$2,300 per acre-foot. Only six sales of Twin Lakes

stock by CLADCO, Aetna, and the Proxy Group (one to Pueblo West in 1972, two to Pueblo in 1972 and 1973, and three to Colorado Springs in 1972 and 1976) accounted for the transfer of over 43,000 shares, or the vast majority of the shares of all Twin Lakes stock.

Other transfers of Twin Lakes stock for nonagricultural users occurred during the mid-1970s. Pueblo West bought a farm with 237 shares of Twin Lakes stock in 1971, for about \$1,400 per acre, including all land, improvements, and water rights. The farm is still in operation and is continuing to use the water rights until Pueblo West wants them. Pueblo West acquired another 117-acre farm with Twin Lakes water rights from a real estate development corporation, but the amount paid is unknown. Colorado Springs bought a total of approximately 500 acre-feet from miscellaneous owners during the summer of 1976 for an average price of over \$2,000 per acre-foot. Aurora acquired approximately 2,500 shares of Twin Lakes stock in 1973 for \$2,675 per acre-foot.

Very little specific price information is available on the sale of other shares of Twin Lakes stock. Small quantities have reportedly been sold to homeowners in mountain resort communities. As an alternative to purchasing less expensive but also less flexible native stream rights and undertaking potentially lengthy and expensive water court transfer proceedings, some individuals have preferred to purchase shares of Twin Lakes stock for prices ranging from \$8,000 to over \$10,000 per acre-foot.⁴³

In 1983 and 1984, the Colorado Foundry & Iron (CF&I) Steel Corporation sold its storage rights in Tourquoise Reservoir to the cities of Colorado Springs, Pueblo, and Aurora. Colorado Springs purchased 17,470 acre-feet of storage rights, plus two direct flow rights totaling about another 4,200 acre-feet, for about \$400 per acre-foot. The city purchased the rights primarily for the reservoir storage space, which it can use to facilitate the exchange, storage, and delivery of water supplies developed from numerous other sources. These sources include water from the Homestake and Blue River transmountain diversion projects as well as various direct flow and storage rights acquired in the Arkansas River basin. The 4,200 acre-feet of direct flow rights that Colorado Springs acquired from CF&I are considered unimportant, as they are too junior in priority to be very dependable.⁶¹

In the fall of 1986 Colorado Springs closed on a deal to transfer 17,500 acre-feet of direct flow and storage rights in a complex transaction involving three different water companies. The package included land, improvements, and water rights in the Henry and Meredith Reservoirs and the Colorado Canal Company. The seller, Foxley and Company, had acquired the property from CLADCO, which had purchased it originally in order to market the shares of Twin Lakes stock associated with the lands. Foxley sold its interest in the companies to Colorado Springs for a total of about \$27.75 million, or slightly under \$1,600 per acre-foot.⁶²

Henry and Meredith Reservoir rights were valuable to Colorado Springs, not only for the deliverable quantities of water, but also for the reservoir storage space. Colorado Springs may store unused water from some of their direct flow water rights in the Henry and Meredith

Reservoirs should there ever be insufficient storage capacity in Pueblo Reservoir. Water stored in these reservoirs is then available to serve downstream users who in turn may exchange their flow rights to Colorado Springs for water upstream in the Pueblo Reservoir.⁶¹

Until recently, Colorado Springs hardly utilized its legally reusable return flow water. A small portion of water has been marketed to downstream users for their groundwater augmentation plans. The price charged for the sale of return flow in 1985 was about \$235 per acre-foot. In 1986 the price was increased to about \$260 per acre-foot. Additional small quantities of return flow have been used for urban irrigation. Most of the water, however, was simply released into the Fountain River where it flowed downstream to mingle with the Arkansas. In recent years, Colorado Springs has begun ambitious efforts to reclaim all of its legally reusable return flow. The city wishes to expand its reuse of return flow significantly by substituting an average of 34,000 acre-feet of return flow per year for stored water in Pueblo Reservoir.⁶¹ Depending upon the outcome of its first return flow case in court, Colorado Springs anticipates reclaiming up to another 30,000 acre-feet of water through similar exchange programs. It is not known how much, if any, of the reclaimed return flow may eventually be marketed to other water users.

The City of Fountain is a small town 10 miles south of Colorado Springs in the Fountain Valley. Fountain used to derive all of its water from the Mountain Reservoir. The city was forced to seek an alternative source when state health authorities ordered expensive renovations in the water treatment system. Fountain first considered purchasing a groundwater wellfield about 20 miles to the east in the Black Squirrel basin, but local opposition successfully blocked the sale. Fountain then developed its own wellfield in another area during the 1960s. With the closing of the area to further groundwater appropriation and the passage of new groundwater management legislation, Fountain had to acquire additional water rights to compensate for its groundwater pumping. Part of its legal obligations are met by releasing water from the Mountain Reservoir. The rest is met through the retirement of water rights associated with Fountain Valley Mutual Irrigation Company water stock, which Fountain has been gradually purchasing for several years. With the completion of the Fountain Valley Pipeline in 1985, Fountain now also has the option of purchasing Fry-Ark water. Fountain has also considered purchasing additional groundwater rights in the area, but the water quality is poor and the asking price for the rights is too high.⁶³

The city of Pueblo is located along the Arkansas River just below Pueblo Reservoir, about 30 miles east of the Front Range. In addition to its participation in the Frying Pan-Arkansas Project and its acquisition of stock in the Twin Lakes Company, it has purchased a number of shares of stock in other ditch companies and has constructed some water development projects of its own. Pueblo's principal water company acquisitions in recent years have been the purchase of storage rights in the Otero Canal Company, the Booth-Orchard Canal Company, and storage and flow rights in the Rocky Ford

Highline Canal Company.⁶⁴ The city also bought storage rights in Tourquoise Reservoir from CF&I Steel Corporation in 1983, paying about \$440 per acre-foot for 5,000 acre-feet of storage rights. Another 5,000 acre-feet of storage rights were sold at about the same time to the City of Aurora for the same price. In two separate transactions in 1967 and 1969, Pueblo paid to the City of Aurora between \$2,500 and \$3,600 per acre-foot for the right to lease up to 2,500 acre-feet of water per year from Aurora, at a normal charge of \$3 per acre-foot.

Pueblo offers its unused reservoir and transmountain diversion water rights for rent each year. Direct flow rights are not rented because their transfer to another user, even for only a season, would require proceedings before the water courts. Pueblo's Twin Lakes water is offered for lease at a predetermined price. A recent large surplus of rental water on the market forced Pueblo to reduce its asking price from \$18 to \$10 per acre-foot. Prices for other types of water are determined on the basis of closed bids solicited by the city. The town of Pueblo West, which also offers water for rent each year, regularly trades information with Pueblo on the bids each has received from prospective buyers. Pueblo generally sets a floor on its rental prices and will not offer water below that minimum price, even if as a consequence it is left with large quantities of unrented water. The city of Aurora regularly leases Twin Lakes water from Pueblo, paying a unit price equal to the highest bid received by Pueblo for its water that year.⁶⁴

Pueblo West is a resort community several miles west of the city of Pueblo near the base of the Front Range. Pueblo West began developing its water supply in the 1960s by drilling several groundwater wells. Most of the wells drew poor quality water, and the potable water available from the wells was not sufficient to support a sizable community. In the early 1970s, Pueblo West purchased shares of Twin Lakes water stock and negotiated an agreement with the SCWCD to store the water in Pueblo Reservoir. The municipality now owns enough water rights to serve a population ten times its current size. Each year the extra water is made available to whoever wants to lease it. The rental prices are determined through closed bids. Real prices since 1982 have varied from as little as \$3 per acre-foot to over \$30 per acre-foot. Pueblo West has never succeeded in renting all of its unused water rights. Since 1982, it has rented as many as 1,680 acre-feet and as few as only 331 acre-feet.⁶⁵

The City of Aurora, a fast-growing metropolitan center just east of Denver, concluded another three major acquisitions of water rights at the close of 1986. A majority interest in the Rocky Ford Ditch Company was acquired, giving the city 8,200 acre-feet of water at a cost of about \$2,500 per acre-foot. Following the successful transfer of water from the Colorado Canal Company by Colorado Springs, Aurora picked up its own 5,600 acre-feet from the Colorado Canal Company, also at a cost of about \$2,500 per acre-foot. Finally, Aurora acquired 45% of the outstanding shares of stock in the Busk-Ivanhoe Ditch Company, yielding about 3,000 acre-feet at a cost of \$3,500 per acre-foot. The city was willing to pay a premium price for the Busk-Ivanhoe stock because

they represent transmountain diversion rights, which are both legally and hydrologically easier to transfer to the South Platte basin than are native flow and storage rights in the Arkansas River.

Other examples of large blocks of water rights offered for sale in the Arkansas River basin include the Bessemer Ditch and the Huerfano-Cuchares Ditch Companies. In 1986 the Huerfano-Cuchares Ditch Company, which had been offered for \$13 million, sold for about \$10 million. The quantity of transferable water rights is currently under study. Historic diversions by the company have totaled about 6,800 acre-feet per year, of which perhaps half may have been used consumptively and are therefore available for transfer. In addition, Huerfano-Cuchares has an adjudicated right to 60,000 acre-feet of storage water, although the reservoir is in need of repair and at the present time cannot hold more than 35,000 acre-feet.⁶⁶

The 10,000 shares of the Bessemer Ditch Company are being offered for \$60 million, or \$6,000 per share. Each share has an average yield of 3 acre-feet. It has not yet been established how much of this average yield may be transferred out of the company service area. Previous to this offer, the market price for the stock among irrigators had been between \$1,200 and \$1,500 per share.⁶⁶

Prospective buyers of water rights in the Arkansas basin have not forgotten the disastrous purchase of water rights by the state Game and Fish Commission in 1971. Up until that time, shares of stock in the Catlin Canal Company, with a long-term annual average yield of 4 acre-feet per share, had been selling for about \$160. The Game and Fish Commission bought 2,097 shares in the company at a cost of about \$320 per acre-foot, intending to transfer the water rights to a large reservoir along the river for fish and wildlife habitat. The remaining stockholders in the Catlin Canal Company successfully opposed the transfer by arguing that their water rights would be impaired. The Game and Fish Commission appealed the decision, which was eventually upheld by the state Supreme Court. Over \$2.5 million (not including court costs) was paid by the State for water rights that could not be transferred for their intended use.⁶⁷

To summarize, market transfers of water occur in Colorado under highly diverse conditions. Appropriated water rights represented by water company stocks having a large service area and approved for multiple uses can be readily transferred. As is apparent from other types of transactions in the Northern and Southeastern Colorado Water Conservancy Districts, market transfers can also be subject to expensive, time-consuming, and complex approval procedures and litigation.

TRUCKEE RIVER BASIN, NEVADA

Description of the Study Area

The market area chosen for study in Nevada includes the Truckee River Basin and adjacent areas in southern Washoe County, Storey County, and parts of Churchill and Lyon Counties. Most of the area's population of

250,000 is concentrated in and around the twin cities of Reno and Sparks, which are located in a valley known as the Truckee Meadows. The Meadows are flanked on the west by the Sierra Nevada Mountains and on the east by the Great Basin. Most agricultural activity is concentrated in the Newlands Project, about 50 miles east of the Truckee Meadows. The Newlands Project, managed by the Truckee-Carson Irrigation District (TCID), was one of the first irrigation projects built by the Bureau of Reclamation in the early 1900s. These areas are shown in figure 5.

The Truckee begins at Lake Tahoe in the California Sierras, crosses the state line into Nevada, and flows east past irrigated farms and ranchlands surrounding the metropolitan centers of Reno and Sparks in the Truckee Meadows. Eventually it approaches the western edge of the TCID near the town of Fernley, where the river turns north to empty into Pyramid Lake on the Pyramid Lake Indian Reservation.

Nevada is the driest and one of the fastest growing states in the United States. Reno and Sparks are regional centers of tourism and commerce and their populations are expanding rapidly. Rights to Truckee River water are highly controversial. Conflicts among the cities, Native Americans, fish and wildlife managers, and irrigated agriculture have continued unabated for most of the 20th century.

An average of approximately 650,000 acre-feet of Truckee River water is used per year in northwestern Nevada. Roughly 50,000 acre-feet is used for municipal and industrial purposes in the Truckee Meadows, while 300,000 acre-feet is used for irrigation. Irrigation uses are divided among farms in the TCID (190,000 acre-feet), and other farms and ranches (about 105,000 acre-feet). About 300,000 acre-feet of Truckee River water flow into Pyramid Lake.⁶⁸ Consumptive use of the water rights along the Truckee River has risen over time, and as a result the quantity of water emptying into Pyramid Lake has declined. Falling lake levels have alarmed sportsmen, conservationists, and especially the Pyramid Lake Indians.⁶⁹

On average, about 375,000 acre-feet of water are used annually by TCID from rights developed on the Truckee

River and on the Carson River, which parallels the Truckee 20 miles to the south. Water taken from the Truckee River by TCID is carried by the Truckee Canal into Lahontan Reservoir, where it mingles with roughly an equal quantity of water from the Carson River before its distribution over TCID's 75,000 irrigated acres. By a joint agreement among the TCID, the State of Nevada, and the U.S. Fish and Wildlife Service, return flows from the Newlands Project are allowed to dissipate in marshlands to the east of the TCID to support the Stillwater Wildlife Refuge.

Approximately 10,000 acre-feet of groundwater are used annually for municipal and industrial purposes in the cities of Reno and Sparks. A small number of domestic users in the Truckee Meadows area outside of Reno and Sparks and a few irrigators use another 2,000 to 3,000 acre-feet per year. There is limited groundwater pumping in the TCID by individual users; the district itself has no groundwater rights. Groundwater quality is highly variable within the Truckee Meadows. It can be very poor in the southern and eastern portions of the area owing to the presence of heavy metals. In some locations, the water is so poor that it cannot be used unless it is mixed with purer water from the Truckee River. Groundwater withdrawals in the Truckee Meadows are carefully regulated by the State Engineer because of the danger that excessive pumping could draw poor quality water into the more potable aquifers.⁷⁰

Market transfers of water in the general area of the Truckee River basin have been confined mainly to the Truckee Meadows. A small number of groundwater rights transfers have occurred in some nearby valleys. Regional water transfers involving the TCID, the Pyramid Lake Indians, and the Stillwater Wildlife Management Area are legally difficult and have not yet been attempted. These areas are nevertheless included in the study because the management of their water resources continues to have a significant impact on the availability of water supplies in the Truckee Meadows water market. Nonagricultural water users located outside of the existing or planned service area of Sierra Pacific generally have had to rely on local groundwater supplies to meet their water demands. Because the basins in northwestern Nevada are closed to additional appropriation, and because exempt groundwater wells are too small and inadequate for most purposes, new water users have had to acquire water rights by transferring them from existing users.

Municipal and industrial customers in the Reno-Sparks area receive gas, water, and electrical service from the Sierra Pacific Power Company, a privately owned utility. The Washoe County Public Works Department provides some water service to outlying communities in the Reno-Sparks area. A few communities have been serviced by private water companies, several of which have been taken over recently by Washoe County. Irrigators outside TCID hold individual decrees for water in the Truckee River, which is distributed to them by private ditch companies. A number of ditch companies once provided Truckee River water to irrigators in the Truckee Meadows. Many of these companies are now inactive because the lands within their service areas have

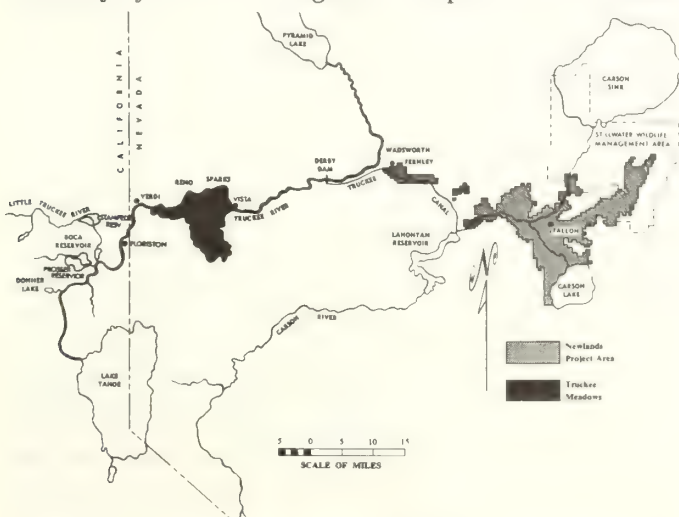


Figure 5.—Northwestern Nevada: The Truckee River Basin.

been developed and their water rights transferred to Sierra Pacific.⁶⁹

Lake Tahoe and Boca Reservoir serve as area-wide regulatory and storage facilities for the Truckee River; in addition, Sierra Pacific operates two small privately owned reservoirs, Donner and Independence Lakes. A third facility, Stampede Reservoir, was originally developed by the Bureau of Reclamation as a multipurpose, supplemental water supply. The water supply, however, was preempted to support fish habitat and has never been made available for municipal use. Sierra Pacific is attempting to work out a compromise solution with the federal government whereby at least some water may be made available to the company.⁷⁰

Water Laws and Institutions

For several decades Nevada has applied the appropriation doctrine for administering both groundwater and surface water resources.⁷¹ The Office of the State Engineer was created in 1903 with the passage of Nevada's first comprehensive water law, passed primarily to provide a method by which the existing rights to appropriated water might be defined, regulated, and protected. Relatively few changes in the basic water laws have occurred since 1939 when legislation declared all groundwaters not hitherto subject to the appropriation doctrine to be explicitly included. Small domestic wells were exempted from regulation. Nevada's general policy towards groundwater has been to restrict withdrawals from a given basin to hydrologically safe yield levels.⁴⁶

In the 1960s, Sierra Pacific began developing groundwater rights in the Truckee Meadows to supplement its surface water rights on the Truckee River during periods of peak demand. Rights to 48,000 acre-feet per year have been appropriated, but this is far in excess of the area's hydrologically safe yield. The State Engineer and Sierra Pacific have agreed to maintain groundwater pumping at 8,000 to 10,000 acre-feet per year while permitting as much as 12,000 acre-feet to be withdrawn under short-term critical conditions.⁷⁰

The State Engineer has primary responsibility for distribution of all water in Nevada except federally decreed stream systems, which are administered by a Watermaster appointed by the federal district court. The federal Watermaster distributes water according to the priority dates of the water rights, and the established operating criteria for the stream system. Under the Watermaster's supervision, water is diverted from the main stream into ditches owned by water companies. The water companies then distribute the water among individual users according to their rights.

The Truckee River is a federally adjudicated stream administered under the Orr Ditch Decree of 1944. About 29,000 acre-feet of water per year were allocated to the Sierra Pacific Power Company, over 230,000 acre-feet per year to the Newlands Project (TCID), and 177,000 acre-feet per year for irrigation on other lands. Another 30,000 acre-feet per year were designated for irrigated agriculture on the Pyramid Lake Indian Reservation.⁷²

The Sierra Valley Water Decree of 1958 confirmed the right of the Sierra Valley Water Company of California to divert an average of 10,000 acre-feet per year from the Little Truckee River. These water rights are also subject to the Orr Ditch Decree and are administered by the federal Watermaster as part of the Truckee River system.

No water was allocated under the Orr Ditch Decree specifically for the purpose of maintaining the level of Pyramid Lake or streamflows in the Truckee River itself. The Pyramid Lake Indians, who derive much of their livelihood from fishing the lakes and rivers, have contested this omission. In recent years they have been partially successful in winning some concessions in their battle to protect lake and stream habitat for two endangered species of fish, the cui-cui and the Lahontan cut-throat trout.

Although water rights under the Orr Ditch Decree were assigned on the basis of prior appropriation, water is distributed on a prorated basis. Minimum levels of flow in the river at selected points along the stream are maintained according to operating criteria set forth in the Truckee River Agreement of 1935.⁷² The operating criteria provide for the servicing of all appropriations on the river and for the proration of all claims in the event of insufficient water supplies. Modified operating criteria are used during drought conditions. The operating criteria become ineffective only during severe droughts, such as occurred during a few years in the 1930s and once again for a brief period in the late 1970s. When this happens, the federal Watermaster may resort to a system of relative priorities.⁶⁸ Under these extreme conditions, the 29,000 acre-feet of water rights assigned to Sierra Pacific have priority over all irrigation rights.⁶⁹

The operating criteria for the Truckee River have been the focus of continuing controversy for many years. Lack of technical information about the river system has exacerbated the conflicts. In an effort to help resolve the disputes, Sierra Pacific hired an engineering consultant to study the hydrology of the Truckee River basin and to produce a model for planning purposes. All major factions have now accepted the authenticity of the consultant's data, although negotiations continue over the choice of priorities and objectives to use in operating the model.⁷³

Guidelines regulating the transfers of water rights in Nevada are few. The primary condition is that the transfer does not impair existing water rights or otherwise appear detrimental to the public interest. The State Engineer's Office oversees any prospective change in the point of diversion or place or purpose of use of any groundwater or surface water right in Nevada, including those on federally decreed streams. A water right is considered a property right and is protected as such. When water rights are granted they are appurtenant to a given piece of land for a specific purpose. Generally, when land is sold all water rights appurtenant to the property described in the deed automatically transfer to the new owner. However, application to the State Engineer may be made to sever the water right from the land to retain it or convey it separately.

In a federally adjudicated stream system such as the Truckee River, the State Engineer consults with the federal Watermaster on administering water rights transfers in the system under the directives of the federal decree. As long as the transfer is compatible with the operating criteria for the river, it may be approved. Water rights transfers on the Truckee River have not been limited to only the consumptive use portion of the right. Temporary water rights transfers (leases) have not been permitted on the Truckee River. The federal Watermaster has opposed leasing water rights, arguing that leasing would overly complicate the administration of the river.⁶⁸

Water Market Activity

No water market activity has occurred within the Pyramid Lake Indian Reservation. The community is unlikely to enter the marketplace because it has had some success in securing minimal streamflows through non-market strategies. Furthermore, the quantity of water the tribe needs to control the level of Pyramid Lake would require a considerable sum of money, even if the water were legally transferable and a sufficient number of willing sellers existed. Relying on nonmarket water transfer strategies, the Pyramid Lake Tribe has effectively been able to gain access to water, although the rights are not formally recognized by the State Engineer.

The Pyramid Lake Tribe has won concessions on two fronts, and in both cases their victories have had an impact on the water rights available for other users along the system. Their first success was Stampede Reservoir, which was built by the Bureau of Reclamation in eastern California in 1970 to aid in regulating the flow of the Truckee River. The reservoir originally was conceived of as a multipurpose water project, but no water has ever been diverted from it for either irrigation or municipal and industrial uses. Since the early 1970s, the federal government has allocated all the water in the reservoir to help maintain the level of flow and the temperature of the Truckee River for fish habitat. The reservoir will continue to be used for this purpose so long as the native trout species in the Truckee River and in Pyramid Lake are considered endangered. Sierra Pacific Power Company had counted on receiving a substantial allocation of water from the reservoir. Appeals by Sierra Pacific and the State of Nevada against this decision thus far have been unsuccessful.

Another success for the tribal community was a change in the operating criteria for the Truckee River system initiated in 1985. Water supplies released for irrigation purposes both inside and outside of the TCID have been reduced by several tens of thousands of acre-feet per year. Conservation requirements for reducing evaporation and seepage losses are being enforced.⁶⁹

Water rights in the TCID are difficult to transfer. TCID is a federally funded and administered project, and ownership of water rights used on project lands by individual water users has been unclear. Financial obligations to the project are based on land ownership and not

water usage. There is no established procedure in the Newlands Project for transferring project assessments with water rights that are transferred off of project lands.⁷⁴ The district's water supply is a mixture of water from two different river systems each of which is administered under its own federal decree. The relative proportions of water from each river system have varied from year to year with changes in relative flow levels in each river. It is thought that any attempt to transfer water rights outside of the TCID would create serious legal and administrative problems for the management of the Newlands Project.⁶⁸

Until recently, no transfer of TCID water rights had been permitted into, out of, or within the district. Federal adjudication of the Carson River in 1983 established the legality of water rights transfers within, but not into or out of, the district.⁷⁵ By mid-1985 about 100 proposed water rights transfers within the district had won provisional approval from the State Engineer.⁷⁴ Final approval of the water rights transfers within TCID are being withheld pending an appeal by the Pyramid Lake Indians.⁷⁵ The outcome of this case will have a strong bearing on whether or not water transfers will become common in the TCID. No price data were collected on transfer of TCID water rights, which are exclusively surface water rights. Groundwater rights in the Fallon area of the district are reportedly selling for about \$300 per acre-foot.⁷³

Sierra Pacific began purchasing irrigation rights to supplement its original Truckee River appropriations in the mid-1940s, and continued to acquire additional water rights actively until 1979. Real prices ranged from a low of about \$35 per acre-foot in 1946 to a peak of about \$160 per acre-foot in the mid-1960s. From 1966 to 1979, the real price per acre-foot for water rights fell steadily. Most of the water rights acquisitions during the period 1946 to 1979 actually occurred between the late 1950s and 1970.

The present water market developed in the Truckee Meadows during the mid to late 1970s when the U.S. Department of Interior refused to provide water and storage rights in the Stampede Reservoir for municipal and industrial purposes. Sierra Pacific had been counting on receiving between 17,000 and 34,000 acre-feet of additional water rights and regulatory storage space in the reservoir for a cost of about \$17 per acre-foot per year. Meanwhile, Sierra Pacific's rate of acquiring additional irrigation water rights from irrigators had been declining as the real price offered by the company to farmers dipped below \$75 per acre-foot. Unprecedented rates of urban growth in Reno and Sparks threatened to outpace Sierra Pacific's capacity to serve them with additional water. In 1978 Sierra Pacific commissioned an independent study of its water resources and projected demands. The report concluded that the current rates of growth in water use in Sierra Pacific's service area would exceed the firm yield of the company's existing water rights inventory and would be insufficient to meet demand within two or three years.⁷⁶

A water crisis hit the Truckee Meadows seemingly overnight. Holders of water rights on the Truckee River

recognized that they possessed a scarce and valuable commodity. Landowners who had until then subdivided their holdings indiscriminately with the water rights appurtenant began to sever the water rights from the land to sell them separately. Sierra Pacific was reluctant to pay the increased costs for water rights. In 1980, the utility raised its offer price for water rights to a range of \$95 to \$135 per acre-foot, based on relative water rights priority dates. Later it raised its offer price to \$140 per acre-foot, and eventually to \$250. The increase, however, was not enough to attract sufficient numbers of sellers, who found many other buyers in the Truckee Meadows willing to pay \$1,500 and more per acre-foot. Water rights acquisitions by Sierra Pacific slowed to a trickle as potential sellers held out for higher prices.

Faced with an impending water shortage, Sierra Pacific began rationing additional water service. New water users were put on a lengthy waiting list pending the acquisition of sufficient water rights. The creation of the waiting list touched off an intense battle between government and industry and between pro-growth and no-growth advocates. Private developers and the cities of Reno and Sparks accused the utility company of becoming a self-appointed regional planning agency.⁷⁷ Environmental groups criticized the cities for trying to grow beyond their means.

Throughout the early and mid 1980s, a series of interactions among Sierra Pacific, private interest groups, the State Public Service Commission, and the State, county, and local governments created new legal and administrative infrastructures to accommodate the pressures for a more efficient, equitable, and workable system of water rights transfers in the Truckee Basin. The new system was largely in place by the spring of 1985. Under a ruling of the Public Service Commission, Sierra Pacific is required to provide water service to approved new developments within 60 days.⁷⁸ Water rights are provided by the appropriate local government (the cities of Reno or Sparks, or Washoe County) through long-term (99-year) leases.^{77, 79}

The water rights inventory of Sierra Pacific and the additional water rights available for purchase in the 1980s in the Truckee Meadows and elsewhere is as follows. Sierra Pacific has water rights with an average yield of roughly 79,000 acre-feet per year. This includes 29,000 acre-feet of originally adjudicated flow rights in the Truckee River, 12,000 acre-feet of groundwater, and 38,000 acre-feet of additional surface water rights acquired since 1944. Approximately 38,000 acre-feet of water rights are still used for irrigation, 28,000 acre-feet in the Truckee Meadows area and 10,000 acre-feet in Sierra Valley, California. Finally, an estimated 32,000 acre-feet of water rights formerly used for irrigation are no longer in use. These water rights are still appurtenant to lands that were incorporated into the service area of Sierra Pacific and were provided with water service without ever having the water rights severed.⁷⁰

Sierra Pacific has determined that the firm yield (the minimum yield from the water rights that could be expected under the worst drought conditions) averages about 58% of the long-term average yield for these water

rights. Sierra Pacific's original appropriation of about 29,000 acre-feet per year, however, is given the highest priority on the river and has a firm yield of 100%.

In accepting water rights in exchange for water service, Sierra Pacific established the following guidelines. The water rights have to produce a firm yield of water sufficient to meet the estimated water demand for the proposed development. Firm yield is defined as 58% of the long-term average yield of the water right. The water rights have to be decreed Truckee River water rights. If the new development is already within the service area of Sierra Pacific, the water right may come from either within or from outside the service area boundaries. If the new development is located on land that the applicant was seeking to have annexed into Sierra Pacific's service area, then the water right has to come from outside the current service area boundaries. Under certain circumstances Sierra Pacific will consider accepting groundwater rights, if they have valid permits and it can be demonstrated that the water is of acceptable quality.

The local governments acquire the water rights they lease to Sierra Pacific from two different sources. Most of the water rights are provided by developers who are required to dedicate sufficient water rights to the local governmental jurisdiction as a precondition for project approval. Sierra Pacific assists prospective buyers of water rights by providing a list of names of interested water rights sellers. The list is periodically updated and is available upon request from the company. The cities are slowly acquiring additional water rights under a special program created by state legislation regarding the disposition of the estimated 32,000 acre-feet of unused irrigation rights appurtenant to lands served by Sierra Pacific. The cities of Reno and Sparks and Washoe County are authorized to acquire by purchase or by condemnation, if necessary, the water rights appurtenant to these lands.⁸⁰ Water rights acquired by the cities are "banked" by the appropriate local government authority until such time as the city or county wishes to use them in support of a particular development project.⁷⁷

Prices for water rights in the Truckee Meadows and outlying areas vary considerably. Groundwater prices usually are low because groundwater quality generally is lower than surface water quality, and legally the rights tend to be more difficult to transfer. Since 1983 Washoe County has been acquiring private water companies serving groundwater to customers in rural areas. It began the program of acquisitions because of concerns about the poor condition of many of the companies and potential health problems posed by their deteriorating facilities. As a condition for taking over the companies, the county generally has required that the owners sell all assets and rights of way necessary to provide water service to existing customers, including water rights, for an amount not to exceed the cost of the initial investment. For the water rights the initial investment might be no more than the cost of the filing fees for the appropriation of the water right, a total of about \$100.⁸¹

In one exceptional acquisition in January, 1984, Washoe County acquired a water company but purchased a quantity of water rights separately from the

other assets. The Trans Sierra Water Company had an appropriated but as yet undeveloped right to pump 2,600 acre-feet of groundwater over and above what it was already pumping to serve its existing customer base. The county was interested in acquiring the rights and entered into negotiations with the company for their purchase. Initially the company offered the rights for \$1,500 per acre-foot, an amount equal to the current price for Truckee River rights. Washoe County refused the offer, arguing that the groundwater rights were not as transferable as surface water rights, were not available for use in the areas of high water demand, and therefore could not be valued equally. Furthermore, the rights had not yet been developed and were in danger of being forfeited. Eventually Trans Sierra relented and sold the rights to the County for \$50 per acre-foot.⁸¹

Other groundwater rights in northwestern Nevada have sold for substantial sums of money. In some isolated groundwater basins near the Reno-Sparks area where development pressures are strong but municipal water service is not readily available, prices have risen to unusually high levels. In recent years, for example, groundwater rights in the Spanish Springs and Lemon Valley areas near Reno and Sparks have sold at prices ranging between \$4,000 and \$10,000 per acre-foot.⁷³

In contrast to groundwater rights, surface water rights in northwestern Nevada are almost always highly valued, although prices still vary. Highest prices are observed for large, consolidated blocks of rights appurtenant to lands located outside the existing service area of Sierra Pacific. Lowest prices are observed for small rights appurtenant to urbanized lands within the Reno-Sparks metropolitan area which are already served water by Sierra Pacific. An independent water rights appraisal conducted in 1984 listed 52 water rights transactions occurring between 1982 and 1984, with (nominal) prices ranging from \$875 to \$2,016 per acre-foot.⁸²

Larger lots of water rights tend to bring higher unit prices than do smaller lots because of the high costs of transacting water rights transfers in the Truckee Meadows. Frequently it is unclear whether land that was subdivided from another parcel that had an original water right decree retained any of the water right. Lengthy and sometimes expensive title searches are often necessary to prove ownership of water rights before they can be transferred. According to Sierra Pacific, the total cost for the title search, the payment of filing fees, and other costs for transferring a water right may be \$1,000 per transaction or more.

A survey conducted in March 1985 by the Public Service Commission found that of the 32,000 acre-feet of water rights identified as subject to SB 323 acquisition, about 16,000 acre-feet were in blocks of less than 10 acre-feet and were the most likely candidates for purchase. The other 16,000 acre-feet involved blocks of 10 acre-feet or more, of which perhaps a dozen holdings were in excess of 100 acre-feet each. Of these 16,000 acre-feet of larger holdings, about 8,000 acre-feet were being retained by developers who wanted them for building projects. The remaining 8,000 acre-feet were held by owners who were willing to sell but were holding out for a higher

price. Of a dozen interested sellers who were contacted with offers of \$1,000 to \$1,100 per acre-foot, none accepted. Four counteroffers were given ranging from \$1,750 to \$2,000 per acre-foot.⁸³

Reno, Sparks, Washoe County, and Sierra Pacific have agreed to offer landowners \$422 per acre-foot for their water rights under the SB 323 acquisition program. The price is based on a market value for the rights of \$1,500 per acre-foot, less all transactions costs. Sierra Pacific leases the water rights from the cities and county for \$422 per acre-foot, plus the costs to the local governments of handling the rights. When the water rights are applied towards a new development, Sierra Pacific passes to the new user its costs of acquiring the water right plus the expenses incurred in doing the title work on the transfer.⁸⁴

As of the end of 1986, the program of acquiring water rights under SB 323 had met with only limited success. Sparks had purchased about 50 acre-feet of rights, and Reno about 325 acre-feet. Most of the potential sellers of water rights contacted by the cities had either failed to respond or had rejected the offer. Apparently there are two reasons for the general lack of response to the program. First, many holders of water rights have resisted selling their rights in the belief that prices will rise significantly in the future. The second is that several private water brokers operating in the Truckee Meadows have been outbidding the cities. Typically, the price offered by the brokers ranges between \$600 and \$800 per acre-foot, less a brokering fee. The brokers assemble several small water rights, each one as small as an acre-foot or less, into a package for resale to a local developer. The price for these brokered packages of urban water rights has exceeded \$2,000 per acre-foot.⁷⁷

Sierra Pacific is actively considering various market and nonmarket alternatives for acquiring additional water rights from sources outside the Truckee basin. The market alternatives include buying surface water rights in Sierra Valley, California, and groundwater rights in Warm Springs and Honey Lake, Nevada. Ranches in Sierra Valley are irrigated by surface water rights from a number of sources, including the Truckee River. Sierra Pacific has considered purchasing land with water rights at prices up to \$2,000 per acre. Because Truckee River water rights tend to be spread relatively thinly over many acres, the company would have to purchase large parcels of land from dozens of different owners to secure an adequate supply of rights. The high cost of the water rights—in excess of \$2,000 per acre-foot, not including pumping costs—local opposition to the purchase, and uncertainty over the legal implications of transporting water across the state line, have diminished interest in this particular alternative.^{70, 85}

A more attractive market alternative for Sierra Pacific is the acquisition of groundwater rights in distant basins. The company is considering two different purchases, one for between 3,000 and 4,000 acre-feet of water rights in the Warm Springs area, 19 miles from Reno, and another for between 10,000 and 14,000 acre-feet in the Honey Lake area, 35 miles from Reno. Prices, which currently are still under negotiation, will probably fall bet-

ween \$500 and \$600 per acre-foot for rights in the Honey Lake area, and between \$1,000 and \$1,200 per acre-foot in the Warm Springs area. Sierra Pacific is negotiating lower prices for these water rights than it is willing to pay for Truckee River rights because of the high cost of treating the groundwater and transporting it into the Truckee Meadows.⁷⁰

To summarize, water prices and conditions for water transfer vary considerably in the Truckee River Basin of western Nevada. Sierra Pacific and the cities of Sparks and Reno are large market participants and exert some influence on water prices within their service areas. Transfer within the Basin are complicated by unresolved Indian water rights claims, separate federal decrees for management of the Truckee River and the Carson River, and ambiguities surrounding interstate transfer and transfer of water developed by Bureau of Reclamation projects.

GILA-SAN FRANCISCO BASIN, NEW MEXICO

Description of the Study Area

The market area studied in New Mexico is the drainage basin of the Gila River, including its major tributary in New Mexico, the San Francisco River. The Gila-San Francisco Basin is a federally adjudicated basin in southwestern New Mexico, bordered on the east by the Continental Divide and on the west by the State of Arizona. Most of the land area in the basin is comprised of the Gila National Forest and the Gila Wilderness, vast expanses of sparsely populated forest and chaparral environments at elevations ranging between 6,000 and 10,000 feet. In the southern and western portions of the basin, where most of the population and most private landholdings are concentrated, elevations are lower and forest gives way to grasslands and high desert. The major urban center in the area is the town of Silver City with a population of about 20,000. Silver City is just outside the Gila-San Francisco Basin, south and east of the Continental Divide in the Mimbres Basin. Towns within the Gila-San Francisco Basin are small and widely scattered. The principle settlements include Reserve and Glenwood in Catron County and Cliff and Redrock in Grant County. These areas are shown in figure 6. The predominant industries in the Gila-San Francisco Basin are mining and ranching. Irrigated crop farming has been on the decline for many years. Since the late 1960s and early 1970s a number of vacation and retirement homes have been built in the vicinity of the Gila National Forest.

About 31,000 acre-feet of groundwater and surface water rights are held in the Gila-San Francisco Basin, roughly 6,500 acre-feet in the San Francisco portion of the basin and 23,500 acre-feet in the Gila portion. The rights in the San Francisco portion are used almost exclusively for irrigation and domestic purposes. The rights in the Gila portion are divided up as follows. Silver City holds over 1,300 acre-feet of water rights of which it is permitted to export the consumptive use portion, or about 800 acre-feet, to the Mimbres Basin. Mining com-

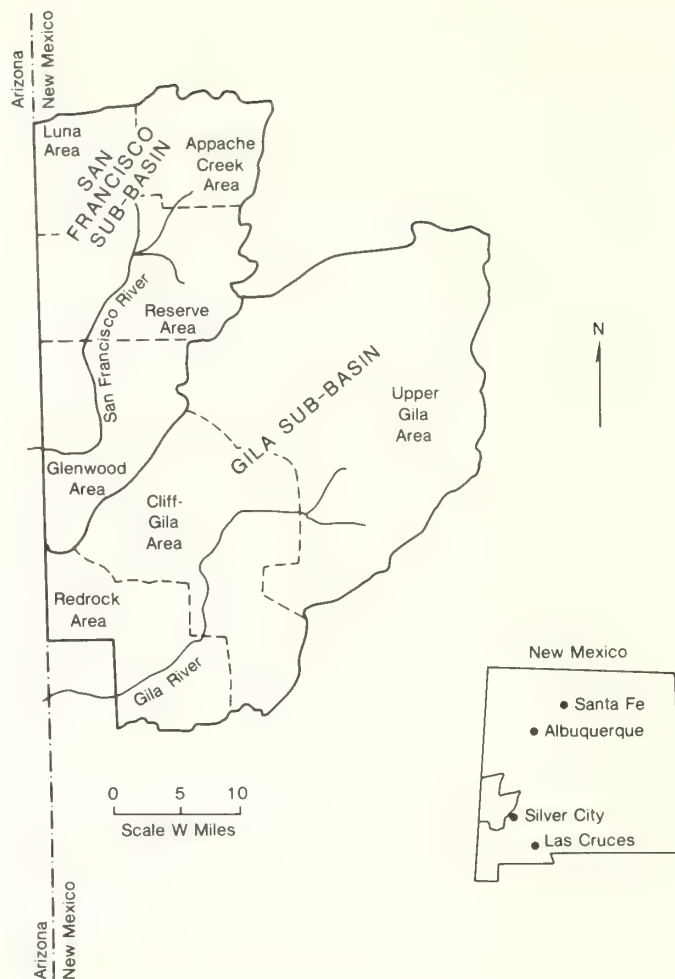


Figure 6.—Southwestern New Mexico: The Gila-San Francisco Basin.

panies hold about 11,800 acre-feet of rights, but their level of consumptive use is considered to be high so the quantity they are permitted to pump is less than this. The remaining 10,000 acre-feet of rights in the Gila sub-Basin are held by households, and irrigators.

Much of the water used in the Gila-San Francisco Basin comes from surface water sources, but groundwater pumping is also extensive. Surface water rights on the Gila and San Francisco rivers and on tributary streams are usually supplied by small private ditch companies. A large block of both surface and groundwater rights is used by the Phelps Dodge copper mine, near the town of Tyrone. The Boliden copper mine, which is still under construction, will use groundwater exclusively for its operation. Silver City and a few other small towns and residential subdivisions operate water treatment and distribution systems that also depend entirely upon groundwater. Most other domestic and commercial water users operate their own private groundwater wells.

Water Laws and Institutions

Virtually all groundwater and surface water rights in New Mexico are subject to the legal doctrine of prior ap-

appropriation. A comprehensive administrative water code, passed by the territorial legislature in 1907 and adopted by the newly constituted state government in 1912, remains the basic surface water law of New Mexico today. Groundwater was first regulated in 1931.⁸⁶

All surface waters and most groundwater in New Mexico are administered by the State Engineer. The State Engineer's responsibilities include all matters relating to the apportionment, transfer, and distribution of water. The State Engineer must approve all new appropriations of water for beneficial use as well as for changes in the place or purpose of existing uses. Jurisdiction of this office over the regulation of water rights includes all surface water rights and any groundwater in declared groundwater basins. The State Engineer designates a particular hydrologic region to be a declared groundwater basin when there is reason to believe that rapid development in the area might impair existing water rights. Most areas in the State are now included in the more than 30 declared groundwater basins.

Anyone in New Mexico who cannot be served by a municipal or domestic water service organization may drill a well for household use. A well that provides water for a single household and irrigates no more than 1 acre of land is usually exempt from state regulation. In declared groundwater basins, however, exempt wells must be registered with the State Engineer. Exempt groundwater rights are routinely granted by the State Engineer in most parts of New Mexico (the Gila-San Francisco Basin being an exception) for indoor and for outdoor household uses such as watering gardens, small orchards, and lawns, washing cars, and filling swimming pools.

In New Mexico, a water right is a property right and inherent in that ownership is the prerogative to change the point of diversion, or place or use of the right. These changes, however, are governed by the overriding question of whether or not the change will impair existing water rights holders. A transferred right retains its priority date and its specific quantity of water so long as the right continues to be exercised.

Although the right to water is transferred automatically with the sale of the land unless reserved in the deed, a water right can be bought and sold separately from the land and sold for a new use in another area. The water withdrawn from use in the first area is adjusted for losses associated with the change of the point of diversion and credited to the water supply in the second area. The new owner is then allowed to draw from the credited supply.

Both groundwater and surface water rights can be sold or transferred. The transfer can be of both location and purpose. In some instances where surface water and groundwater resources are considered integrally related, the State Engineer may allow transfers from surface appropriations to groundwater appropriations on a limited basis. Under these circumstances, a new appropriation of groundwater may be permitted under the condition that the appropriation acquire and retire, that is, withdraw from use surface water rights in quantities sufficient to compensate for the effects of groundwater pumping.⁸⁷

Water right owners can lease all or part of their right for not more than 10 years without affecting their original water right. New Mexico law states that a water right unused for 4 years is subject to forfeiture. A major benefit of leasing the right is that the owner avoids losing the right because of nonuse. The lease may be effective immediately or may be designated for future use in so far as that use does not accumulate or impair other water users.⁸⁷

In the mid-1960s, the State Engineer formally declared the Gila-San Francisco Basin following the U.S. Supreme Court's adjudication of the lower Colorado River basin in *Arizona vs. California*.⁸⁸ The U.S. Supreme Court divided the Gila-San Francisco Basin into two separate sub-basins, corresponding to the respective drainages of the Gila and the San Francisco Rivers, and specified the maximum quantity of water that could be consumptively used from each of the two rivers before they flowed into Arizona. The court also divided each sub-basin into a number of areas, and specified the maximum number of allowable irrigated acres within each area. There are four areas in the San Francisco sub-Basin: Luna, Apache Creek, Reserve, and Glenwood. There are three areas in the Gila sub-Basin: Upper Gila, Cliff-Gila, and Redrock. Following the issuance of the U.S. Supreme Court's final decree in March 1964, the State of New Mexico adjudicated all water rights in the basin, and the process was completed by 1967. Finding that the total existing water rights were somewhat less than the limit imposed by the Supreme Court, limited filings for additional appropriations were allowed to continue for a short time. The basin has been closed to additional appropriations since about 1967.⁸⁹

During the state adjudication proceedings in the mid-1960s, the State Engineer identified the exact acres of irrigated land, domestic households, and commercial enterprises that were putting water to beneficial use and had a valid claim to a water right. Commercial and industrial water rights were determined on the basis of their historical levels of use. Irrigation water rights (per acre) were determined on the basis of three different measures: the maximum allowable diversion right, in any 1 year; the maximum 10-year rolling average diversion right, and the consumptive use portion of the right. These measures vary throughout the Gila-San Francisco Basin but are uniform within each one of the seven areas. Domestic well rights are fixed at 3 acre-feet per year throughout the Gila-San Francisco Basin. There is no recognized consumptive use portion to a domestic well right.⁸⁹

As a federally adjudicated basin, the Gila-San Francisco faces particularly stringent controls on the allocation, use, and transfer of its water rights. Appropriation of water rights for outside domestic use is not permitted even though this is routinely granted in closed groundwater basins elsewhere in New Mexico. Households with exempt groundwater wells cannot maintain lawns, gardens, orchards or otherwise use any water outdoors unless additional water rights are acquired to serve that purpose. The Gila-San Francisco has an active market for individual household water rights.⁹⁰

Water rights transfers are permitted within the Gila-San Francisco Basin although they are subject to several restrictions. Water rights are not transferable into or out of the Gila-San Francisco Basin and are not transferable between the Gila and San Francisco sub-Basins. However, quantities of water equal to the consumptive use portion of any water right may be physically transported into or out of the basin or from one sub-basin to the other. Any diversion right in any quantity may be transferred within the same area. Only the consumptive use portion of a water right may be transferred between areas within the same sub-basin. Surface water and groundwater throughout the Gila-San Francisco Basin are considered to be interchangeable and the rights to one may be converted into the other—the point of diversion for a surface water right may be converted into a groundwater well, and vice-versa, usually without altering the quantity or priority of the right. In some cases where a surface water right is of very junior priority or is drawn from an intermittent stream where the full extent of the right is not generally accessible, the diversion right may be adjusted downwards when converted into a groundwater appropriation.⁹¹

Irrigation rights may be transferred for other purposes of use, but water rights assigned to non-irrigation purposes may not be transferred for irrigation use. In contrast, domestic well rights may be transferred anywhere within their respective sub-basins without changing the quantity of the right. Industrial water users who acquire irrigation rights are generally limited to divert no more than the consumptive use portion of the right.⁹²

Water Market Activity

Water market activity in the Gila-San Francisco Basin has occurred since the basin was closed to additional appropriation in the mid-1960s. Thousands of acre-feet of water were transferred from irrigation to mining within the first few years, mostly in nonmarket transfers of water rights from a large ranch to a newly opened copper mine, both of which were owned by the Phelps Dodge Corporation. The ranch and its water rights had been acquired and developed by Phelps Dodge before the closing of the basin. The Phelps Dodge development holds over 11,000 acre-feet of water rights, which is equal to about half of all the water rights in the Gila sub-Basin and over two-thirds of all the water rights in the Cliff-Gila Area. Nevertheless, the market for the remaining water rights has been very active, with most activity involving the trading of the remaining irrigation water rights in the Cliff-Gila Area. Buyers for the water rights in the Gila-San Francisco Basin include other irrigation users, individual households, the town of Silver City, and a few smaller mines and commercial enterprises. The major commercial-industrial buyer of water rights since the Phelps Dodge acquisitions has been the Exxon Corporation and its successor, the Boliden Minerals Company, which acquired several hundred acre-feet of water rights in the early 1980s for a new copper mine 20 miles north of Silver City.

In 1986 Phelps Dodge announced that it had purchased Kennecott's interest in the Chino mine in the Mimbres Basin, and that it planned to phase out its mining operations at its Tyrone mine in the Gila-San Francisco Basin. Approximately half of the more than 11,000 acre-feet of water rights owned by Phelps Dodge in the Gila-San Francisco will no longer be used for mining within 10 years, and within 20 years the mine will be shut down completely, freeing up all of the water rights for alternative uses. The mine has considered transferring some of its rights to domestic purposes on company land that may be sold for retirement homes, but it is unlikely that all or even most of Phelps Dodge's water rights could be used for that purpose. The future of the supply and demand for water rights over the next few decades in the Gila-San Francisco Basin is therefore highly uncertain.⁹³

San Francisco Sub-Basin

Almost all water rights in the San Francisco sub-Basin are used for irrigation or municipal and domestic purposes. A few small mills and a small mine are the only commercial water users in the area. Market transfer of water rights did not begin in the San Francisco sub-Basin on a significant scale until the mid to late 1970s, about 10 years after they began in the Gila sub-Basin. Most transfers have been in small quantities of 3 to 6 acre-feet or less. Prices for water rights in the late 1970s were about \$500 per acre-foot; prices rose to as much as \$3,000 per acre-foot before leveling off. Prices have fallen below \$1,500 per acre-foot since 1983, when a major flood washed out many irrigated lands and a number of holders of irrigation rights chose to sell their water rather than invest in reestablishing their farms.⁹³

Gila Sub-Basin

A substantial portion of the water rights in the Gila sub-Basin are controlled by three major entities: the Phelps Dodge Corporation, the Boliden mining company, and the town of Silver City. The remaining water rights are distributed over many individual holders, mostly in quantities of less than 50 acre-feet. The most active trading has been in small quantities of rights, often 1 acre-foot or less of rights at a time. The earliest sale of water rights dates to 1966 when a parcel of water rights were sold for about \$1,800 per acre-foot. Real prices for water rights increased steadily through the 1970s, reaching over \$4,000 per acre-foot by 1980. Since 1980, prices generally have declined to a range of \$1,500 to \$2,500 per acre-foot.

Price increases in the Gila sub-Basin during the late 1970s may have been attributable to the entrance of the Exxon Corporation into the water market. In 1979 and 1980, Exxon negotiated with about 25 different owners of land and water rights for the sale of as much as 1,200 acre-feet of irrigation water rights for transfer to mining. Roughly half of the transactions involved the sale

of only water rights, and the other half involved the sale of land and water rights together. In 1982 Exxon sold to Boliden most of its assets, including much of the water rights.⁹⁴

Exxon contracted to buy the land and water rights through 5-year, annually renewable options. Options prices for the properties varied between about \$3,300 and \$6,600 per acre of land (about \$2,000 to \$4,000 per acre-foot of water at a rate of about 1.6 acre feet per acre). Annual payments to keep the option contracts current ranged from 6% to 10% of the option price. Generally these payments were not credited against the option price. In a few cases, a down payment in the first option year equal to about 20% of the option price substituted for annual payments. Some options were exercised as early as 1981, but most sales were not concluded until late in 1984. Two or three options were cancelled.⁹⁴ Exxon negotiated each option contract separately. There appears to be no direct correlation between either the option price and the size of the sale, or between price and the inclusion or exclusion of appurtenant land along with the water rights.

Water Leasing

Rental price data from 1963 to 1983 were collected on four leases in the Gila sub-Basin and on one in the San Francisco sub-Basin. Prices ranged generally between \$100 and \$250 per acre-foot with no evidence of any long-term trend either up or down. Rental prices for water in the Gila-San Francisco Basin appear to stand at roughly 10% of the current sales price for the rights.

Water Rights Acquisition by Silver City

Silver City owns water rights in both the Mimbres and Gila-San Francisco Basins. Most of the rights were appropriated and developed at a very low cost, but some were purchased at high market prices. Until 1982, nearly all of the water rights owned by Silver City were concentrated in two groundwater wellfields: the Franks field in the Gila-San Francisco Basin and the Woodward and Anderson fields in the Mimbres Basin. Since 1982, groundwater rights in two new areas in the Mimbres Basin have been acquired by the city.⁹⁵

Rights to develop groundwater on the Franks Ranch were acquired by contract in 1945.⁹⁶ Silver City agreed to pay the landowners a rent of about \$3.50 (nominal dollars, not adjusted for inflation) per acre-foot of water pumped and transported off the ranch. The contract had no termination date and there was no inflation adjustment clause. The price paid for the water has not been increased since it was established in 1945. A similar contract signed in 1954 allowed Silver City to develop the Woodward field.⁹⁷ The Woodward contract was amended in 1967 to increase the nominal dollar rental price from \$3.50 to about \$5 per acre-foot. Silver City has the right to pump and transport about 1,500 acre-feet per year from Woodward Wellfield, approximately

800 acre-feet per year from the Franks Wellfield, and an additional 400 acre-feet per year from the Anderson wells.⁹⁸

Additional groundwater rights have been acquired by Silver City in both the Gila-San Francisco and Mimbres Basins. All purchases of water rights in the Gila-San Francisco Basin have been in the Gila sub-Basin. In 1981 the city purchased 78 acre-feet of water rights with a consumptive use of 43 acre-feet at a cost of about \$3,000 per acre-foot of transportable (consumptive use) water. In 1984, the city purchased another 131 acre-feet of transportable water at a cost of \$2,900 per acre-foot.⁹⁹ In 1985, the city acquired 32 acre-feet of transportable water for slightly more than \$2,200 per acre-foot. All of these water rights were successfully transferred to the Franks Wellfield, in the Cliff-Gila Area, and the water is being pumped over the Continental Divide into the Mimbres Basin. There have been two recent water rights acquisitions in the Mimbres Basin. In 1982, Silver City paid about \$1,500 per acre-foot for 193 acre-feet of water rights.¹⁰⁰ In 1985, 1,433 acre-feet of water rights were acquired for about \$2,200 per acre-foot.⁹⁵

To summarize, water rights transfer in the Gila-San Francisco Basin can be readily arranged, with lower transactions costs than in many other areas studied. Silver City and the mines hold the majority of water rights in the basin, and the number of potential market participants is relatively small. The announced closing of the Phelps Dodge Mine has cast a cloud of uncertainty over the future supply and demand for water rights in the basin. Nevertheless, market sales and rentals of water rights among irrigators and between irrigation and non-irrigation water users continue to occur.

LOWER SEVIER RIVER BASIN, UTAH

Description of the Study Area

The market area chosen for study in Utah is the Lower Sevier River Basin of west-central Utah. The Sevier River begins in the highland plateaus of southwestern Utah and flows north for about 150 miles before turning south and west for a short distance to terminate in Sevier Lake. The area lies within the sparsely populated, isolated, and extremely arid Sevier Desert. Average precipitation is less than 8 inches per year. The principal population center is the small town of Delta, with approximately 5,000 residents. It lies in the northeastern corner of Millard County, about 140 miles southwest of Salt Lake City. Other small towns near Delta are Hinckley, Sutherland, Deseret, and Oasis. Also included within the study area are the towns of Lynndyl and Leamington, located along the Sevier River 15 and 20 miles north of Delta, respectively. The lower Sevier River Basin is shown in figure 7.

Approximately 50,000 acres are irrigated in the vicinity of the northern bend of the lower Sevier River. Agriculture, the mainstay of the local economy, is the primary water user in the area. Alfalfa and alfalfa seed are the major products. A significant quantity of acreage is also

devoted to barley and other small grain crops. A major new water user in the area is the Intermountain Power Project (IPP)—a large, coal-fired, electric power generating facility—about 10 miles north of Delta. Currently under construction, IPP will retain several hundred permanent employees when it begins full-scale operations in 1987.

Four mutual ditch companies cooperatively manage most of the surface water supplies within the study area. The Delta, Mellville, Abraham, and Deseret ditch companies are collectively known as the DMAD companies. A fifth company, the Central Utah Irrigation Company, distributes water out of the Sevier River upstream from the DMAD system. The Gunnison Bend, DMAD, and Sevier Bridge Reservoirs operate on the lower Sevier River. Gunnison Bend, the smallest reservoir with a storage capacity of 4,500 acre-feet, is owned exclusively by the Abraham and Deseret Companies. The DMAD Reservoir, with a capacity of 11,500 acre-feet, is owned by all four of the DMAD companies. Sevier Bridge, the largest reservoir with a storage capacity of 235,000 acre-feet, is owned jointly by the DMAD companies and the Central Utah Irrigation Company.¹⁰¹

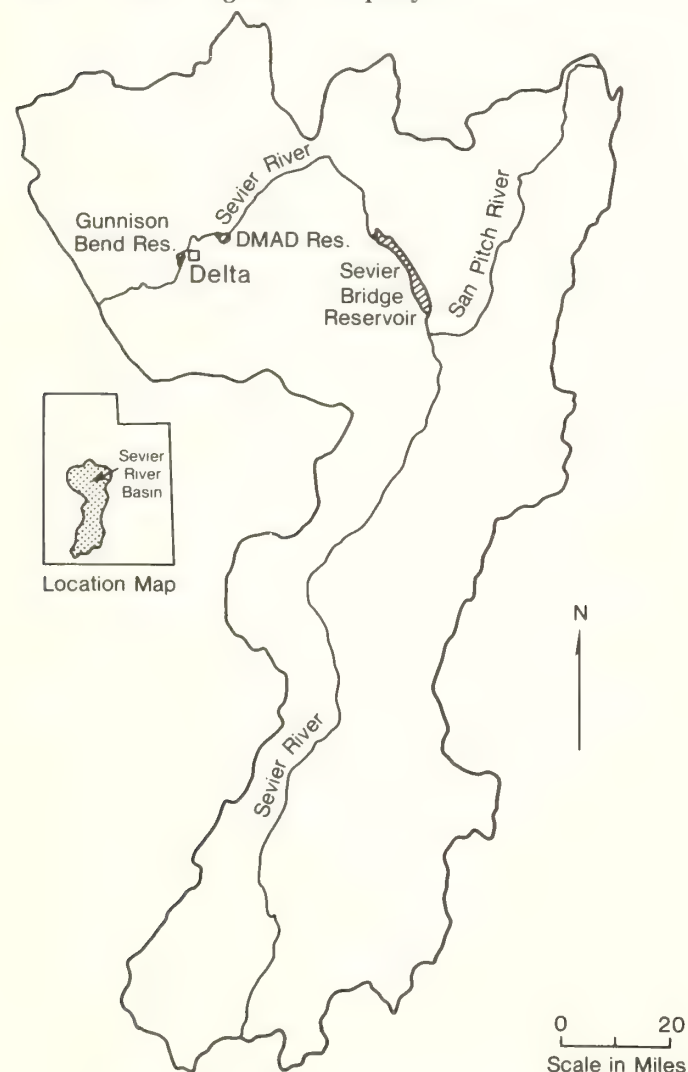


Figure 7.—Central Utah: The Lower Sevier River Basin.

On average, about 120,000 acre-feet of water per year are delivered through the DMAD system. Most of the supply comes from direct flows in the Sevier River and from storage water in the Gunnison Bend, DMAD, and Sevier Bridge Reservoirs. Supplemental water is pumped from several shallow groundwater wells jointly owned and operated by the DMAD companies. Groundwater is pumped into the river to maintain minimum flows and also to reduce salinity levels. As much as 28,000 acre-feet of groundwater per year may be diverted into the river although the volume pumped usually is much less.¹⁰²

The high level of salinity in the Sevier River prevents the water from being used for human consumption. Groundwater quality, however, is generally good throughout the basin. Hence, groundwater is the only source of water for domestic, municipal, and most commercial water users. Groundwater is also used to supplement surface water supplies for irrigation during critical periods.

Water Laws and Institutions

The doctrine of absolute priorities was not followed in Utah because early Mormon leaders gave greater weight to proportionate sharing of water shortages. When rights to Utah streams were established, each claimant was assigned proportionate shares of the flow. The shares assigned to each canal were based on priority of appropriation—the canals that had first diverted water and put it to use in irrigation water were given preference over later canals—though this principle was far from absolute. Time priority was modified considerably by the apportionment of the variable water supply by fractions instead of by physical volume. In this way, the effects of drought were spread over all users instead of only the most junior appropriators.¹⁰³

To prevent the over-allocation of water supplies, Utah instituted a system of primary and secondary rights. In general, primary water users are ensured adequate water supplies to meet all demands even during periods of drought, while holders of secondary rights may not always be able to take delivery of their prorated allocation. This division of water rights into classes was peculiar to Utah in the Western United States. This permitted more equitable sharing of the costs associated with drought than was possible in systems that used absolute time priorities.¹⁰³

Groundwater rights and transfers are controlled carefully in the Delta-Lynndyl area. The groundwater basin has been closed to major additional appropriations since the late 1970s. Water rights of less than 2 acre-feet per year for private domestic use are the only groundwater appropriations still permitted.¹⁰⁴ All lands surrounding the town of Delta and lying east and south of the Sevier River are considered to be within a "high impact" part of the basin. This is where most of the area's population, growth pressures, and economic activity have been located, especially since the arrival of IPP. Groundwater rights transfers are permitted within and

out of the high impact area, but no water rights can be transferred into the area from surrounding areas. The State Engineer also distinguishes between shallow and deep groundwater wells when managing water rights. The best water quality is found in wells drawing from deeper groundwater aquifers. Transfers of rights are not permitted between wells that draw water from different hydrologic formations in the basin. High-quality groundwater within the high-impact portion of the basin is scarce and highly valued.¹⁰⁵

Nearly all of the irrigation water used in Utah is distributed through organized irrigation entities, most of which were established by Mormon pioneers. The successors of these early cooperative organizations are called “mutual water companies” and are the most common type of private irrigation company in Utah. Water rights represented by stock in a nonprofit mutual irrigation company are not appurtenant to the land upon which the water is used. Individual stockholders are not subject to state laws regulating the beneficial use of water rights. They may own as many or as few shares of water stock as they wish, regardless of whether they own sufficient land on which to use the water. A farmer who has a right to more water than he plans to use in a given season or in a given crop rotation may rent his right to a farmer who wants it. An individual may own water stock without owning any land at all and rent out the entire portfolio of water rights every year. Conversely, a farmer may own land and own no water stock and rent the desired quantity every season. The only condition on the use of the water transferred is that it be used within the service area of the mutual stock company.

Water rights represented by mutual water stock can be transferred between farmers simply by transferring the stock. The transfer of stock representing water rights does not require administrative proceedings before the State Engineer to change the point of diversion or place of use of the water. Such proceedings are required in transfers of water rights not represented by mutual company stock. Water rights not represented by stock, are appurtenant to the land for which the appropriation was made, although they may be severed from the land and sold separately. Unless specifically reserved by the grantor, appurtenant water rights automatically pass with a sale of the land.¹⁰⁶ The transfer of water stock outside of the service area of the mutual stock company requires the filing of an application before the State Engineer requesting a change in the point of diversion. If such a change is not within the boundaries of the controlling irrigation company, an administrative hearing is required. However, such changes are usually allowed if they do not interfere with the rights of others.

Water rights in the lower Sevier River Basin were adjudicated under the Cox Decree of 1936.¹⁰⁷ Local mutual ditch companies had already been in existence for many years. Water rights were assigned to each water company on the basis of current use and not prior appropriation. The timing and distribution of proportional shares of the streamflow were specified, along with formulas for prorating water supplies to all users during drought years.

Water is allocated by the governing boards of each of the DMAD companies, who meet each spring to determine the water “credit” to be issued on each share of outstanding water stock. The size of the credit is based on projections of yields from storage and flows along the lower Sevier. Stockholders are given water accounts that function much like a bank account. Water may be withdrawn from the account at any time during the irrigation season, or deposits may be registered by transferring water from another stockholder’s account. DMAD permits owners or renters of company water to carry over any part or all of their holdings to the following irrigation season, less 20% to account for evaporation losses. Water may not be carried over for more than a single year. This option enhances flexibility for the individual farmer in managing his water resources, although there is some risk involved in carrying over water rights. If the storage capacity of the reservoirs is reached at the beginning of the following irrigation season, all carryover accounts are erased and water credits are reissued to all stockholders based on the total available water supply.¹⁰⁸

Water transfers among water users in the DMAD service areas have been common for several decades. Sales and rentals of water among shareholders within individual companies have occurred since the early 1900s. In about 1950, the DMAD governing boards instituted an agreement to permit informal seasonal transfer (rental) of water between companies. Normally, the transfer of water among different mutual stock companies would require proceedings before the State Engineer. In this case, however, the State Engineer waived the proceedings because the DMAD companies are located near the end of the Sevier River where no downstream users could be impacted by any transfer or change in use of the water in the system.¹⁰⁹

Seasonal intercompany water transfers among the DMAD companies continued without formal legal sanction until 1980. In 1980, upon approving the change application to transfer DMAD and Central Utah company water to IPP, the State Engineer finally declared that the points of diversion and place of use for the four DMAD companies were interchangeable.¹¹⁰ Multiple use permits were granted for all the water rights transferred, allowing the seasonal rental of water unused by IPP back to irrigators. The DMAD company secretary works closely with the River Commissioner for the lower Sevier River to ensure that all water accounts “balance,” and that the total appropriations by each of the DMAD companies does not exceed the legal limit of its prorated shares.¹⁰²

Rentals are handled in the same fashion whether the renter wishes to transfer water to land within the same water company service or to land within the service area of another DMAD company. The prospective renter submits a card describing the requested transfer to the DMAD company secretary. Provided that sufficient water credit is left in the individual’s water account for that season, the quantity of water to be rented is debited against the lessor’s account and credited to the lessee’s account. Water is usually rented in acre-foot units, but

the parties may sometimes choose to rent shares of water stock instead. Individuals renting water stock have the option to use the water in the current irrigation season, or to take the risk of carrying the water over into the next season.¹⁰¹

Water Market Activity

Management of the DMAD companies has been highly integrated since at least the early 1960s. There is no longer any practical distinction between owning shares of stock in one company or another. Although the historical average yield per share of stock differs, on a per acre-foot basis the market price for water represented by a share of stock is similar among the four companies. In 1985, the price for water represented by any one of the companies' stock was approximately \$350 per acre-foot.

Water rights prices between 1974 and 1985 exhibit no trend either up or down except for a brief period between 1979 and 1982, when the introduction of the IPP to the Delta area caused a speculative boom in land and water rights. IPP paid over \$2,400 per acre-foot for one large package of groundwater rights and water company stock. Prices exceeded \$1,000 per acre-foot for other sales of water stock occurring at about the same time. By about 1982, the speculative bubble subsided and water stock prices began to return to their former levels.

The package of 45,000 acre-feet of water rights purchased by IPP for its power generating station was composed of 5,400 acre-feet in groundwater rights and 39,600 acre-feet in water company stock. The stock comprised roughly 20% of all the water rights owned by the DMAD companies and 85% of the rights owned by the Central Utah Irrigation Company.¹¹¹ Many different sellers were involved in the transfer, and most of the water rights were sold in relatively small lots. There were 565 individual contracts signed to purchase water company stock, averaging about 60 acre-feet per contract. Another 31 contracts were signed for the sale of groundwater rights with an average of 174 acre-feet per contract.¹¹²

Water rights were transferred to IPP via a seller's collective called the Joint Venture. The Joint Venture was formed after a core group of organizers announced IPP's interest in purchasing water rights and advertised for a collective bargaining coalition in the local newspapers in 1978. Anyone owning stock in the DMAD or Central Utah companies or groundwater rights in the Delta or Lynndyl areas was invited to participate in the sale to IPP. Participants were allowed to offer prorated quantities of water rights for sale, established as fixed proportions of water rights owned by each prospective seller.¹¹³ Individuals were free to offer more than their assigned quantity of water rights for sale, but they had to find other participants who were willing to reduce their allotments by a compensating amount. This led to the development of an active market in sales options. Option prices for the sale of water rights to IPP through the Joint Venture are reported to have sold for as much as \$650 per acre-foot in the late 1970s.¹¹⁴

Groundwater rights in Utah are not quantified volumetrically; rather, they are specified in terms of a flow rate. In order to determine how much groundwater could actually be transferred to IPP, the State Engineer had to determine the consumptive use of groundwater in the areas where the sales were to take place. The State Engineer issued an interlocutory order (the order is not final, pending further hydrologic studies) stating that the consumptive use portion of the groundwater rights in the affected areas was only about half of the average volume diverted.¹¹⁴ IPP had specified in the negotiations that it would only pay for the volume of water that was transferable, not the total volume of the rights. Option prices for groundwater rights reportedly fell by at least half, to about \$300 dollars per acre-foot. Nevertheless, sufficient groundwater water rights were still offered to complete the water rights package wanted by IPP. No final order has yet been issued by the State Engineer. If the interlocutory order stands, the farmers who sold groundwater rights to IPP will have to retire twice as much irrigated acreage as they originally intended. The Joint Venture is prepared to sue the State Engineer if the order is upheld.¹¹⁴

IPP bought groundwater rights for two different purposes. One was to supplement the supply of surface water rights for its power generating operations. The 5,400 acre-feet of groundwater rights acquired for this purpose were purchased from the Joint Venture for the same unit acre-foot price as was paid for the water company stock. A second bundle of groundwater rights were purchased from private individuals to create a "water bank" for the town of Delta to support urban growth.^{115, 116} New developments in the Delta service area must now either provide sufficient groundwater rights to transfer to Delta or pay a raw water fee in order to get hooked up to the town water system. The fee, \$1,000 per acre-foot, is based on the average nominal price paid by IPP for the water rights bank, \$960 per acre-foot, plus a \$40 handling charge. As projects are built and the new users pay Delta for withdrawals from the water bank, Delta reimburses IPP for the cost of acquiring the rights.¹¹⁶

Real prices for groundwater rights have fallen since 1980. Excluding IPP's purchases from the Joint Venture, prices in 1980 and 1981 ranged between \$900 and \$1,200 per acre-foot. Since 1982, groundwater rights located near Delta have sold for about \$700 per acre-foot. Groundwater rights located outside of the high-impact portion of the Delta area basin range in price from \$300 to \$500 per acre-foot.¹¹⁷

Shortly after concluding the sale of the water rights, IPP announced that it would scale back the design of the facility from four power generating units to only two. IPP now expects to use only about 20,000 acre-feet of its 45,000 acre-feet of water rights. The excess water rights will be retained in anticipation of future plant expansion. Unused water supplies will be rented back each year to individual water users in the irrigation companies. Traditionally, water has been rented for one season at a time in the lower Sevier basin. Since IPP has such a large quantity of water rights that will not be used

in the foreseeable future, the company is considering making arrangements for long-term leases of some of the water.¹¹⁸

IPP has become the dominant renter of water in the DMAD system. The long-term impact of IPP on the water rental market may not be known for several years. In 1979, a relatively dry year, DMAD water rented for nearly \$30 per acre-foot. In 1980, the year before IPP began renting water, flows in the Sevier River were high and the real price of rental water subsequently fell to less than \$8 per acre-foot. During the following 2 years flows were closer to the average, but real rental prices only rose slightly to about \$9 per acre-foot. Coinciding with the IPP purchase, the Sevier River system entered upon an unprecedented wet cycle that persisted into 1985. The rental market resumed in the middle of the 1986 irrigation season, but water was still abundant, trading activity light, and rental prices low.

Water rental prices between 1948 and 1982 ranged roughly between about \$7 and \$75 per acre-foot. Real prices generally increased from a range of \$7 to \$20 per acre-foot in the late 1940s and early 1950s to a range of \$20 to \$75 in the mid-1950s through the mid-1960s. Since the late 1960s the rental price has declined again to a range of \$8 to \$25 per acre-foot. Rental prices have varied tremendously from one year to the next. Between 1953 and 1954, for instance, rental prices increased from \$11 per acre-foot to \$26. Between 1967 and 1968, real prices fell from \$50 per acre-foot to \$24. During the 1986 season, prices ranged between \$3 and \$5 per acre-foot.

A study of water rental price behavior conducted between 1946 and 1963 in the Delta area indicates that fluctuations in water rental prices are strongly related to the hydrologic cycles of the Sevier River.¹¹⁹ Rental prices tend to be high in dry years when water supplies are low, and low in wet years when water supplies are high. Rental activity is busiest during the spring and summer months, and the volume of rentals varies with the total supply of water. The rental volume is lowest in very wet years because supplies are more than adequate for most stockholders and demand for additional water is low. The volume of water rented is also low in very dry years when supplies are scarce and prices are high enough to cut short demand for supplemental water. Rental activity appears to be the highest in moderately dry years when the demand for water is strong and the supply is more flexible.

To summarize, market activity in Utah's Lower Sevier River Basin demonstrates how water rights represented by mutual water company stocks can be transferred with minimal transaction costs. The entrance of Intermountain Power Project into the market, first as a major water buyer and now as the principal lessor of water to irrigators, is an interesting case study of a dominant market participant's impact on water prices and transfers. The Utah market also provides an opportunity to observe both sales and rentals of groundwater and surface water.

MARKET PRICES AS MEASURES OF VALUE

A measure of value used by a public agency to evaluate supply augmentation projects should fully reflect poten-

tial beneficiaries willingness to pay for incremental increases in the available water supply, as well as any positive or negative side effects (externalities) of the supply increase on individuals or groups in the region. This section outlines economic concepts helpful in understanding the role of market prices as measures of value and identifies three sources of concern: (1) limitations economic theory places on prices as measures of value; (2) the effect of specific market characteristics on prices as measures of social value; and (3) practical considerations that would confront an agency seeking to use market prices as measures of value. These concerns are discussed, along with their implications for using market prices to value incremental flows from public lands.

THEORETICAL CONCERNS WITH PRICES AS MEASURES OF VALUE

Prices in a perfectly functioning competitive market will reveal buyers' willingness to pay for the marginal (the last) unit purchased. Figure 8 shows hypothetical urban, agricultural, and aggregate demand functions for water at a fixed point in time. The downward slope of the curves reflects the economic concept of diminishing marginal utility. The value of the first units of water made available is high, as water in excess of precipitation is essential to economic activity in the arid West. However, as more units of water become available to a particular water user, that individual or firm is willing to pay less and less for each increment of water. Different types of water users have somewhat different demand curves. Urban residents (illustrated by D_U in figure 8) attach a higher value to the small quantity of water they use than most farmers would be willing to pay for that same quantity of water. However, irrigated agriculture also has a downward sloping demand curve for water (D_A in figure 8). The negative slope reflects the fact that the first quantities of water available to a farm are the most valuable because they will be applied to crops for which the highest returns can be obtained. Additional water will be applied to the next most profitable set of crops, and so on. The aggregate water demand curve, D_A , is the horizontal summation of the agricultural and urban demand schedules. Given a supply curve represented by S_1 , the market clearing price for water occurs at P_1 . Note that the market price lies above the unit value water users would place on additional supplies if the supply curve shifted out to S_2 . Willingness to pay for units of additional water could be substantially lower than P_1 , depending on the shape of the total demand curve to the right of Q_1 . As figure 8 illustrates, even in a perfectly competitive market, observed prices serve only as an upper bound for what current market participants might be willing to pay for additional supplies.

Figure 8 portrays water demand, supply, and price formation in a static framework. As population and income levels grow or agricultural commodity prices and production technologies change, demand and supply curves shift and new prices evolve. As these changes occur, prices emerging from previous demand and supply relationships could either overestimate or underestimate the

marginal value of water supply increases in the future. A more complete discussion of demand and supply conditions surrounding water in the Southwest can be found in Kelso et al.

In a smoothly functioning competitive water market, price is uniquely determined by convergence of buyers' and sellers' marginal values. However, water transactions do not take place in well-functioning competitive markets that generate prices fully reflecting the costs and benefits of transactions to all parties affected. In actual market transactions, a negotiated price will lie between the buyer's maximum willingness to pay for units of water exchanged and the minimum amount the seller is willing to accept in payment for water transferred. In a transfer from a farmer to a city water supply organization, for example, the lowest price acceptable to a farmer (the reserve price) would be based on the value of the marginal product of water in agriculture if only a portion of the farm's rights are sold or the value of average product if rights for the whole farm are sold. Also, farmers may view water rights as an appreciating asset and add speculative value to their reserve price, as Gardner and Miller find in analysis of Colorado water market transactions.¹²⁰

Young notes that only a small fraction of agricultural water use is influenced by urban demands expressed through market processes.¹²¹ Much irrigation water is supplied under public project contracts and is insulated from market pressures because most public project water is not readily marketable. Also, irrigation water supplies may not be attractive to urban buyers because they can be expensive to deliver and treat for municipal uses in comparison with alternative sources of supply. For all these reasons, market prices will typically lie above the marginal value of water in irrigated agriculture.

A distinction must be drawn between private and social measures of value. Under competitive market con-

ditions, price negotiated between a buyer and a seller of a water right reflects the marginal value of the units of water exchanged to each party and thus can serve as an indicator of water value for the agents involved in the transaction. A social measure of value, however, also takes into account impacts on parties affected by the transaction who were not part of the price negotiation process. This could include neighboring well owners whose pumping costs are adversely affected, fishermen whose trout habitat is disrupted, future water users whose access to water will be curtailed because of current market activities, or local governments which experience declining tax bases when water sales shift resources out of the local economy.

MARKET CHARACTERISTICS AND PRICES AS MEASURES OF VALUE

Several market characteristics may prevent observed prices from representing social values; e.g., inequities, externalities, imperfect competition, and uncertainty. Table 1 describes these characteristics and provides examples of each in the market areas studied.

Market prices may arise from a distribution of income and access to water that is considered inequitable. Prices generated in water markets inevitably reflect the prevailing income distribution and allocation of water rights. In a market setting, water users with more water and dollars have more "voice" in the marketplace than those with less water and money. In public elections each citizen receives one vote with which to influence the outcome of the election. In water markets, participants "vote" with their dollars and their water rights to influence the outcome of the market allocation process. Therefore public agency use of market prices to measure water's value may not be consistent with distributional objectives of water policy. Controversies regarding Indian water rights in the Southwest illustrate the need for attention to equity issues.

Three additional concerns relate to efficiency issues connected with prices as measures of value: (1) if water transfers positively or negatively affect third parties and these effects (externalities) are not taken into account in market decisions, then prices will not reflect full social values. Prices observed in water markets give the upper bound of an increment in supply only to the extent that those prices represent all uses of the water affected by the increment in supply. Prices are unlikely to be generated for instream water uses, such as recreation, hydropower production, and provision of aquatic habitat; (2) if one or more water users, suppliers or government agencies can significantly affect prices or restrict transfers (imperfect competition) then observed prices may deviate from maximum willingness to pay for marginal units of water; (3) lack of hydrologic and legal information regarding future water availability and transfers can distort market prices, as can uncertainty regarding future government programs and policies. Uncertainty reduces willingness to pay when individuals cannot ascertain what legal rights and restrictions are associated with a particular water right or transfer.

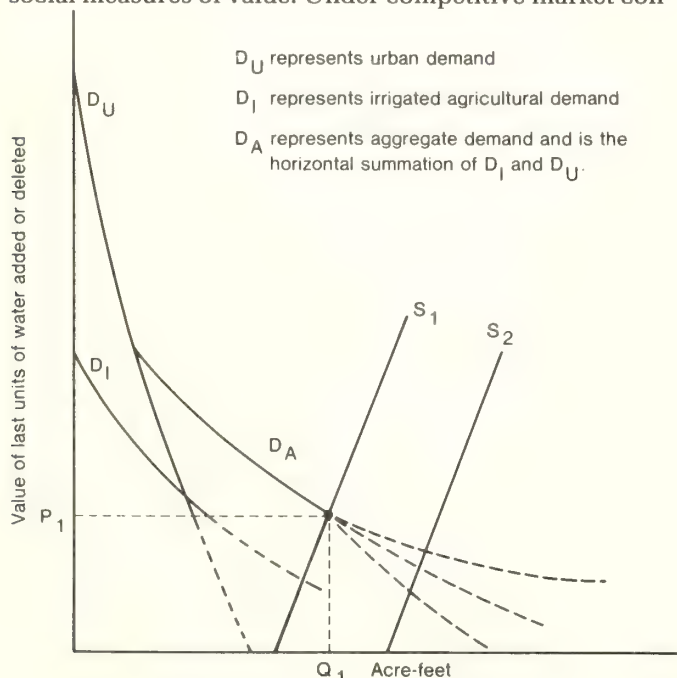


Figure 8.—Water demand and supply.

Table 1.—Water market characteristics, definitions and examples.

Imperfect competition and market restrictions: Market participants or public agencies restrict price levels and other conditions of market transfer, and observed prices may reflect these restrictions.

Example: In northeastern Colorado, municipal water departments and water districts are under public pressure not to profit from renting their unused water supplies back to farmers. Most renters simply rent the water at cost, which may be well below the market clearing price.^a

External effects of market activities (externalities): Market prices do not take into account the values of parties external to the price negotiation process or impacts on third parties.

Example: In the Lower Sevier River Basin of Utah, changing water use patterns by the Inter-mountain Power Project will improve water quality for irrigators by reducing salinity in the river.^b

Uncertainty: Uncertainty regarding future water supplies, demand, and the legal framework that governs water transfers will affect market decisions and observed prices.

Example: The legal framework that governs water use and transfer in Arizona is still evolving, and important legal issues related to transfer of specific types of water rights have yet to be clarified.^c

Significant quantities of additional water supplies were denied to users in Nevada when the federal government decided to use Stampede Reservoir for maintaining fish habitat in the Truckee River instead of allocating the water for consumptive purposes. The ensuing scramble for alternative sources of water has helped push water rights prices to unprecedented levels.^d

Equity and conflict resolution: Economic and legal barriers to market participation can create inequitable access to water. Water allocation decisions may serve as a form of conflict resolution and be made on political rather than economic grounds. Market prices may not fully reflect distributional and political considerations.

Example: Many traditional instream uses of water have never been legally recognized and are increasingly threatened by increased consumptive uses of offstream. In southwestern New Mexico, unique riparian habitat in the Gila River is endangered by a proposed dam.^e Pyramid Lake Indians in Nevada have no water rights to protect their traditional fishing grounds, and have resorted to extensive litigation to maintain minimum flows in the Truckee River system.^d

^aHowe, Charles W., D. Schurmeir, and W. Shaw. 1982. *Innovations in water management: An ex-post analysis of the Colorado-Big Thompson Project and the NCWCD*. University of Colorado, Boulder, CO.

^bClark, Rodney. 1979. *Intermountain power project water supply acquisition*. Presented to the Intermountain Power Association, Salt Lake City, Utah.

^cBush, David B., and Bonnie C. Saliba. 1987. *Dealing for water in the west: Pots of gold or wooden nickles?* Department of Agricultural Economics working paper. University of Arizona, Tucson, AZ.

^dPersonal conversation with Rick Moser, Water Resources Engineer, Sierra Pacific Power Company, Reno, Nevada. 1985.

^ePersonal conversation with George Jackson, Real Estate Broker, Silver City, New Mexico. 1987.

Equity and Conflict Resolution

In market areas where Indian nations hold a significant portion of water rights, absence of Native American participation in water market activity implies that the values of a substantial water interest group are not reflected in market prices. In any region where potential beneficiaries of augmentation are not active market participants, information regarding yield augmentation impacts on nonmarket participants will be necessary for a thorough evaluation of supply augmentation proposals.

Allocation of water to a specific area or group may have political and conflict resolution value to a region, above and beyond measurable economic benefits. Both the Central Arizona and the Central Utah Projects are viewed by some observers as devices for resolving conflicts among water users rather than as economically rational water supply augmentation measures.

Water transfers are often a lower cost alternative for providing water to new users. However policies that encourage market transfers from one sector to another

(agriculture to cities, for instance) may involve political and social costs as income, employment, and tax base shift with water from one sector to another. Decision-makers sometimes implement supply augmentation projects when water transfers might be a lower cost alternative for providing water to expanding uses. In these situations it could be inferred that the conflict resolution and other political values stemming from supply augmentation are perceived to justify the project.

External Effects of Market Activities

Laws and institutions in each market area seek to minimize the impact of water transfers on neighboring water users. Examples of rules that seek to prevent externalities include well-spacing regulations, requirements for consent by others in the affected watershed to proposed transfers, and requirements for engineering studies to demonstrate no third-party effects. Such rules are designed to protect traditional water uses by focus-

ing on return flow levels for surface water or drawdown for groundwater. They are less effective in preventing impairment to nonconsumptive uses of surface water, such as instream recreation. Market prices will not reflect negative side effects of transfers on uses which are not represented in market activities.

External beneficial effects of market activity on third parties do occur. For example, transfer of Colorado-Big Thompson units from irrigators to cities (which have lower consumptive use and are upstream of irrigated areas) has increased return flows for users downstream of the cities—including the irrigators who sold the rights to the cities in the first place. Positive side effects of water transactions may not be reflected in market prices. In valuing incremental flows from public lands, the degree of negative or positive effects of market activity needs to be examined, and observed market prices adjusted accordingly for use as measures of value.

Imperfect Competition and Market Restrictions

The market areas studied differ tremendously in numbers of buyers and sellers, relative influences of particular buyers and sellers, frequency of transactions, and degree of institutional restrictions on market activities. In both the Truckee River and the Lower Sevier River Basins large utility companies are dominant market actors and influence water rental and sales prices. In the Gila-San Francisco Basin and in the neighboring Mimbres Basin a few large mining companies own the largest blocks of water rights. It is not possible to identify precisely the effects dominant buyers or sellers have on prices. In some cases, they seem to function as price setters, giving price signals that are followed by other market participants. However, in the Truckee River Basin, efforts by Sierra Pacific in the early 1980s and current efforts by the cities of Reno and Sparks to purchase water rights at reduced prices have not noticeably affected market prices. With respect to implications for using market prices as measure of value, the presence and degree of imperfect competition needs to be evaluated on a case-by-case basis. If there is a consistent and significant discrepancy between prices emerging from negotiations involving the large volume buyers and sellers and negotiations that do not involve them, then further study will be necessary to determine reasons for the discrepancies and to identify which market prices (if any) are an appropriate reflection of water values.

The numbers of buyers and sellers and frequency of transactions affect the quantity of price data available. A specific price may be a more reliable measure of water value if there are a large number of transactions that confirm that price as typical. In a region with sporadic market activity and spotty price data, use of market prices should be supplemented with non-market information to estimate water values for water.

The seven market areas studied differ tremendously in institutional restrictions on market activity. For instance, in Utah water rights represented by irrigation company stock are readily transferable within the serv-

ice areas of the DMAD companies with minimal paperwork and administrative proceedings, and need not be tied to a specific parcel of land. In contrast, some water rights in Arizona may be transferred only under carefully specified conditions, and irrigation rights cannot be transferred separately from the land.

Within any given market area, different water rights may be subject to different guidelines on change of ownership, purpose of use, location, and leasing. For example, Type II rights in Arizona may be transferred separately from the land to which they are appurtenant but must be transferred in their entirety so that a right holder may not sell only a portion of his rights. Arizona irrigation rights are strictly appurtenant to land but farmers may sell portions of (rather than the entire quantity of) their land and irrigation rights. Colorado transmountain diversion water from the Colorado-Big Thompson project is much more transferable than transmountain diversion water from the Frying Pan-Arkansas Project in the southeastern part of Colorado. Local transfers of Lower Sevier River surface water rights in the form of mutual company stock transactions are less complicated than transfers of groundwater rights in the Lower Sevier Basin.

These examples illustrate the fact that generalizations among areas regarding marketability of water rights must be made with caution. Within each state studied there are varying degrees of restrictions on market activity that apply to different kinds of water rights. Similarities among state water laws are found in the themes of water's appurtenancy to land, requirements for beneficial use, and prior appropriation. It is not the overriding legal doctrines that differ greatly across states but rather the interpretation and implementation of those doctrines as manifested in local water management institutions.

Legal, Hydrologic, and Economic Uncertainty

All markets studied are characterized by varying degrees of uncertainty and access to market information. Arizona and Utah markets provide contrasting examples of this. The Arizona Department of Water Resources keeps records of Type II water rights holders, which may help buyers and sellers to find one another, though there is no central clearing house for communicating bids and offers. Recorded transfers are few in number relative to other water markets. Because Arizona water markets are still in the early stages of development, potential buyers and sellers have little experience and historical information on which to base expectations about water values and market processes. In the Lower Sevier Basin irrigation company records provide information on ownership and rental patterns, and company offices have served as informal clearinghouses—helping prospective buyers, sellers, and renters to find one another. Historical records on the hydrologic cycle of the river system, along with careful reservoir management, give water users a basis on which to form expectations about future water flows and availability.

Hydrologic uncertainty is inevitable in surface water markets as supplies cannot be predicted each year until winter snowpacks are studied to predict spring runoff and river flows. This uncertainty is mitigated to varying degrees by storage facilities and interbasin diversion projects. One of the principal objectives of the C-BT Project is to reduce uncertainty associated with erratic and seasonal surface water flow. Uncertainty affects groundwater markets when there is incomplete knowledge on aquifer capacity, rates of overdraft, and other factors that affect expectations regarding the long-term expense of pumping groundwater.

Hydrologic uncertainty affects how much individuals are willing to pay for a water right. Senior surface water rights are generally more valuable than junior surface water rights that are more vulnerable to seasonal and year-to-year variations in flow. For example, Sierra Pacific made price offers for water rights based on their priority dates—with the most junior rights valued 25% less than the most senior rights.⁷⁷

Uncertainty regarding future water demand and the health of regional economies and water-using industries is inevitable and affects market prices. Water prices rose sharply in the Lower Sevier Basin with expectations that Intermountain Power Project would build a large power plant in the area, bringing increased population and water demand. Prices dropped when the power plant and development boom turned out to be much smaller than anticipated. The short run marginal value of water to irrigators rises and falls with crop prices, and the interest of mines and other industries in acquiring water rights fluctuates with the profitability of those industries. Economic uncertainty affects market prices because prices reflect economic expectations and conditions. With respect to valuing water, this implies that one needs to be aware of economic factors that influence observed prices. A short-run rise in prices due to expectations that a new industry may enter the area would not be a good indicator of water values until prices stabilize after expectations either are or are not realized. In contrast, a long-term price effect from stagnation of a water-using industry (copper mining in parts of the Southwest, for example) would be a valid component of water value in the affected region.

To summarize, there are several potential problems in considering water market prices as measures of value appropriate for use by a public agency. First, in an “ideal” market the observed price represents market participants’ willingness to pay for the marginal unit of water currently available. Willingness to pay for *additions* to the existing water supply could differ substantially from the market price. Second, current market activities and institutions may favor some water users over others, creating inequitable access to water and income-earning opportunities. Third, market activities may generate externalities—effects of water use and transfer poorly reflected in market prices. Some externalities arise because potential beneficiaries of water supply increases are not market participants and impacts on their well-being would not be reflected in market prices. Finally, observed prices may be influenced to

varying degrees by imperfect competition and legal or hydrologic uncertainties.

PRACTICAL CONSIDERATION IN USING MARKET PRICES

Assuming that there are no a priori reasons to suppose that market prices are not appropriate measures of water value, what practical problems would confront an agency seeking to use market prices to value water?

The diversity of institutional settings in which market activities occur affects the practicality of using prices as measures of value. First, there is no a priori reason to believe that prices emerging in one market setting will be relevant to water values in a different area. Second, even within the same market region, prices observed for one type of water right do not necessarily convey useful information about the value of a different type of water right. This underscores the importance of identifying the institutional structures that will govern allocation and use of augmented yields as a first step in valuing those yields. If market prices are used to establish the value of increased flows, they should be prices that emerge from an institutional setting and type of water right closely resembling the institutions and water rights that will characterize augmented yields. Additional flows cannot be valued until decisions have been made regarding who has the right to use the water and under what conditions the right can be exercised and transferred.

Another difficulty involves identification and description of the various water “commodities” in the area of study.¹²² Careful study of state water law and local water management institutions is necessary to define and differentiate these commodities.

Gathering information about market prices is a time consuming task. Transactions must be identified from records of state engineers or water agencies. Such records rarely include price data, so contact must be made with market participants or knowledgeable observers to learn about prices associated with specific transactions. Much “digging” may be needed to uncover a representative price, though in some areas the “going” price for a certain type of water right is a matter of common knowledge. This is true of Colorado-Big Thompson unit prices, for instance.

Another practical problem involves deciding which prices are most appropriate for valuing water from supply augmentation projects. In any market region there are many prices for water arising from various types of transactions. For instance, in the lower Sevier Basin prices emerge from rental and sales of irrigation company stocks and occasional purchases of surface or groundwater not represented by company stocks. In Arizona, water prices arise from sales of Type II non-irrigation rights and purchases of farmland with appurtenant irrigation rights. All observed prices may vary seasonally and from year to year, as supply and demand for water fluctuates. Which, if any, of these prices (and at what points in time) are appropriate for a government agency interested in valuing water? In general, prices

should be selected that most closely reflect the conditions under which increased supplies will be made available and the uses to which the water will be applied. If "new" water represents a permanent increase in regional water supplies, then market sale prices for the intended purpose of use might be appropriate. If additional water will be made available sporadically on a seasonal basis, then short-term rental prices may be more appropriate as a reference value. Rental prices vary across seasons and between water uses, and the price selected should correspond to the season and the use for which the additional water will be available. Additional supplies made available in the dry, high-demand months will naturally have more value than the same volume made available in high-flow low-demand seasons.

COMPARISON OF PRICES ACROSS MARKET AREAS

Table 2 summarizes price data collected on purchases of perpetual water rights in the various areas studied. Price observations over time are reported in terms of

equivalent 1986 dollars paid per acre-foot of long-term average yield on diversion rights acquired by the buyer.

Understanding price differences across market regions is complicated by the differing economic forces dominant in each region—energy development in the Lower Sevier Basin versus rapid urbanization in central Arizona, for example. Although it would be difficult to demonstrate empirically, Arizona, Colorado and Utah water prices may be dampened by expectations of new water supplies from the Central Arizona Project, the Windy Gap Project, and the Central Utah Project, respectively. Anticipation of new water supplies can decrease incentives to bid water away from existing uses.

Prices tend to be lower when the predominant buyer for the water rights is irrigated agriculture, as with DMAD stock in Utah, and nonagricultural users do not compete significantly for water with agricultural users. Prices tend to be higher where expanding nonirrigation water users are buying water rights and supplies are constrained through institutional barriers, physical supply limits, or both, as in the Gila-San Francisco Basin of New Mexico and the Truckee Meadows in Nevada.

Table 2.—Weighted average prices for representative sales of perpetual water rights, in constant 1986 dollars per acre-foot.

Year	Arizona ^a		Colorado ^b		Nevada ^c	New Mexico ^d		Utah ^e	
	Avra Valley	Type II	C-BT	Twin Lakes	Truckee River	Gila	San Francisco	DMAD	Groundwater
1961			130		150				
1962			150		140				
1963			220		170				
1964			370		150				
1965			440		130				
1966			530		160	1,790			
1967			560		160				
1968			600		150	1,300			
1969			850		140				
1970			920	900	140				
1971	430		860	1,400	130	1,630			
1972	420		860	2,400	120				
1973			930		2,400	120			
1974			1,050		110	1,240		330	
1975	570		1,090		100				
1976	570		1,330	2,300	90	1,150		300	
1977	630		2,540		90	1,420	510	550	
1978			2,590		80	3,210	480	550	
1979	700		3,050		70	2,070	440		
1980			3,600	11,820		3,270		2,440	2,440
1981			2,990	10,950		2,990	1,110	1,200	1,150
1982			1,880		470	1,780	510	750	680
1983			1,600		1,730	1,460		430	
1984	870	560	1,460		1,570	2,520	1,460	430	740
1985		920	1,080			2,050	1,140	350	710
1986	630	1,430		8,180			1,210		
1987		1,000				1,810	1,110		

^aData on the sale of Type II nonirrigation groundwater rights were obtained from investment managers, real estate developers, and attorneys. Data on Tucson's acquisitions of Avra Valley land and water rights were provided by city officials.

^bData on sales of C-BT units were obtained from real estate brokers and from public water districts and municipal water agencies. Most price data for Twin Lakes stock were made available by the towns and cities which purchased the rights in the mid and late 1970s. Estimates of earlier market prices were provided by local individuals knowledgeable about the sales. Recent price data were collected from a private attorney.

^cSummary information on water rights acquisitions and prices up to 1979 were available from records provided by Sierra Pacific Power Company. Data on purchases since 1979 were gathered from reports filed by Sierra Pacific with the Nevada Public Service Commission, attorneys, engineers, and other private individuals.

^dDescriptive data on water rights transfers, excluding price information, were available from records maintained by the New Mexico State Engineer. Price data from a sample of these records were collected by contacting individuals involved in the transactions. Records of water rights purchases by Silver City are public information.

^eSales of groundwater rights and ditch company water stock were collected from real estate brokers, attorneys, bankers, and other private individuals. Quantities and prices of water rights purchased by the Intermountain Power Project is public information.

The interaction of shifting supply and demand for water rights along with the variety of institutional settings found among the study areas cause many different types of price responses to be observed. In southern Arizona, where declining groundwater tables and high energy prices have made water resources scarcer than in many other areas studied, water rights prices remain relatively low. Institutional uncertainties involved in transferring water rights, and the existence of alternatives to water rights transfers (the primary alternative being water service from the Central Arizona Project) reduce incentives for market transfers.

Northeastern Colorado provides an example of how perceptions of water scarcity may rapidly increase water rights prices even though long-term supplies remain relatively inexpensive and abundant. A speculative boom in the mid-1970s drove real prices for water rights to unprecedented levels by the early 1980s, although the gradual transfer of water rights from agricultural to nonagricultural use continued without any major change. Widespread concern that increasing urban water demand was quickly outstripping supply led to sharp increases in prices. Gardner and Miller¹²⁰ suggest that prices peaked at values equal to the capitalized marginal demand for water by municipal users. Agricultural water rights holders believed that they each had a high probability of being able to transfer their water rights to a high-valued municipal or industrial water use. For a brief period of time the opportunity cost to agricultural water rights holders of retaining their water rights was equal to the value of the water in urban uses.

Shifts in demand for water rights, or the perception of future shifts in demand for water, has led to rapid water rights price changes in other market areas as well. The impact of a large new water buyer can be observed in Utah water prices as the Intermountain Power Project entered the Utah market in the late 1970s. Prices in the Gila-San Francisco Basin, which had been slowly rising for a number of years, took a sudden turn upwards in the late 1970s when the Exxon Corporation began to acquire water rights for its new mining operation.

It is instructive to consider not only what forces drive water rights prices up, but what forces allow them to fall. Water rights prices in northeastern Colorado probably fell at least partially in response to the construction of the Windy Gap Project in the early 1980s. It is also likely that declining interest rates, the onset of recession, and a faltering farm economy (leading to an increase in the volume of water rights offered for sale) all contributed to the decline in water market prices. In Utah, the scaling back of the IPP to one-half its planned size cut into the speculative bubble that had risen around the project and prices fell. The stabilization of water rights prices in Nevada may be a signal that panic buying of water rights has slowed since private and government organizations agreed upon a system to assure an orderly transition of water rights from agricultural to municipal use. In New Mexico, nominal water rights prices have stabilized and real prices have declined since Exxon (and Boliden) completed their acquisition program.

Every market studied is influenced to some degree by one or more of the four market characteristics discussed earlier and summarized in table 1. In addition, the practical considerations discussed earlier affect every market to varying degrees. Prices for irrigation rights in Avra Valley, Arizona, for example, emerge from transactions between a single buyer (the City of Tucson) and a limited number of potential sellers (Avra Valley farmers). Recorded prices include land and all improvements. It is unclear what the City will do with the land and improvements and it is therefore difficult to assign a value to the water, as distinguished from the value of the whole property. The water value picture in the Tucson area is further complicated by uncertainties surrounding Indian water rights. The 1982 Southern Arizona Water Rights Settlement Act gave the Tohono O'odham Tribe rights to 76,000 acre-feet of water annually, to be delivered by 1992. The Act provides for leasing of tribal water rights to water users within the Tucson Active Management Area under specific conditions and with the approval of the Secretary of the Interior.¹²³ The potential (as yet unrealized) for the participation of the tribe in Tucson area market activities creates a great deal of uncertainty regarding future water supplies and prices. Given these considerations, current market prices do not appear promising as a measure of water value useful to a public agency.

One of the clearest implications of this research is that observed prices, even where they are easily discoverable, should not be used as measures of value until price formation processes and market characteristics have been thoroughly studied. Such an analysis will typically find that observed prices deviate from a social value of water, suggesting that market information be supplemented by nonmarket measures to assess water values.

NONMARKET INDICATORS OF WATER VALUES

Gibbons notes¹²⁴ there is a pressing need to understand water values across economic sectors. Examination of marginal benefits in competing uses would identify disparities in value and potential for promoting more efficient water use. She outlines several approaches to estimating water values in the absence of appropriate market prices. Contingent valuation approaches elicit value information directly from water users. Inferential approaches rely on market-like transactions to infer water values. If adequate price and quantity data are available, a demand curve can be constructed and marginal values estimated at various quantities demanded. Information on physical productivity of water in a production process can be used to construct production functions and to estimate water's marginal value product, given a specific output price. Budget information on production processes can also be used to impute the residual fraction of total output value to water inputs, if all other inputs are paid at their marginal productivities.

Techniques for estimating the marginal value product of water in agricultural production generally rely on programming methods because of the absence of a wide

range of observed water prices for agriculture. Kelso et al.⁷ used linear programming to develop aggregate marginal demand curves for irrigation districts in Arizona and used these demand functions to compare the value of water in agriculture and related sectors of the economy. Howitt et al.¹²⁵ used a quadratic programming model of field crop production to derive a demand schedule for irrigation water in California's Central Valley. Gardner and Miller¹²⁰ computed the marginal value product of irrigation water in the C-BT service area by a residual computation method, subtracting the costs of all inputs except water from gross farm income.

A number of researchers have developed models of municipal water demand. Howe and Lineweaver¹²⁶ in an early study using cross-sectional data from 21 metropolitan areas, found that price elasticity of demand differed substantially between indoor and outdoor use, as well as between eastern and western metropolitan areas. Methods of estimating urban demand functions continue to be refined. Martin et al.¹²⁷ critiqued the use of conventional regression analysis to estimate demand in areas where water rates follow a block rate schedule, and outlined an interactive regression procedure that produces unbiased estimates of demand function coefficients in a block rate setting. Based on these estimates, their study concluded that real price is an important (though not the only important) component affecting consumer demand in Tucson.

Methods for valuing water in recreational and other instream uses are less well developed. Krutilla et al.¹²⁸ described a procedure to estimate the instream energy value of increased flow from augmentation projects. Martin and Cory¹²⁹ commented on this study, emphasizing the importance of comparing water augmentation projects to agricultural water transfer policies in terms of both net social benefits and the incidence of benefits and costs on taxpayers, agriculture, and municipal and industrial interests. Daubert and Young¹³⁰ applied contingent valuation methods to instream flows and found that seasonal reallocation of flows between irrigation and recreation could increase social benefits associated with surface water use.

Lack of household, industry, and farm level data on water use is a major constraint on widespread use of water demand functions as an aid in valuing water for agricultural, industrial, and residential uses. Lack of widely accepted methodologies, along with absence of data, make estimation of instream water values difficult. Supplementing market prices with nonmarket information on water values can be a difficult and time consuming process. However, inferential and contingent valuation techniques have been applied to wildlife, scenic amenities, recreation opportunities, and air and water quality. Research attention needs to focus on adapting these methods to valuing water in alternative uses.

SUMMARY AND IMPLICATIONS

Western water transfers take place under diverse institutional, economic, and hydrologic conditions. Water

markets are characterized by various degrees of imperfect competition, third-party impacts, hydrologic and institutional uncertainty, and distributional effects. These characteristics affect the appropriateness of market prices for use as measures of value. Are prices set or constrained by government policies or dominant market participants? If so, then market prices are not competitively determined. Do market transfers impose uncompensated costs or benefits on third parties? If so, then observed prices do not include values associated with the transfers. Are transfers constrained by physical, institutional, and economic uncertainties? If so, then the level of trading and the performance of the market will tend to compensate for these uncertainties, and this process may distort prices as a measure of water values.

While nearly all market prices deviate from an ideal measure of value, observed prices can provide a rough indicator of the marginal value of additions to regional water supplies if the additional volume of water made available is small relative to the region's total supply. For small supply increases, observed prices may approximate current market participants' marginal willingness to pay for additional water supplied. However, market prices still will not reflect nonmarket water use and third-party impacts of market activities. When the additional volume of water is significant relative to existing supplies, estimation of water's marginal value is more difficult. Marginal values for substantial additions to supply could differ significantly from current market prices. The possibility that substantial increases in water supply could attract new water users into a region and change the structure of demand for water must be considered. For instance, rapid urban growth in southern Arizona is stimulated by the perception that the Central Arizona Project ensures a reliable and adequate regional water supply for expanding cities.

Institutional arrangements that govern allocation, use, and transfer of water determine who bears the costs and who reaps the benefits of water supply development. Information regarding how much new water will be available to various user groups, at what prices, and under what restrictions on use and transfer is essential to the valuation process. Owing to the complex nature of water rights in many regions, it is possible that the transactions costs associated with allocating of new water could exceed the marginal value of that water.

Estimating benefits of additional water availability, using market prices and nonmarket information on water values, is only one step in evaluating a supply augmentation proposal. The impacts of the proposed project must be identified. Will the project affect the well-being of regional residents, apart from the increased water supply? Project side-effects involving environmental quality, employment and recreational opportunities must be included in evaluating the costs and benefits. Will the supply augmentation project affect relative income and access to water among farmers, municipalities, Native Americans, or other major water interest groups? Projects that aid in resolving conflicts and accomplishing regional distributional objectives may have social or political value not typically reflected in economic evalua-

tions. The overall merits of water supply enhancement must be gauged by weighing estimated benefits against total costs associated with the project. Above all, supply augmentation proposals must be compared with alternative water management strategies, including increased water conservation and transfer of existing supplies from lower valued uses to higher valued uses.¹²⁹ Only augmentation projects demonstrated to be the lowest cost alternative for achieving policy objectives should be approved.

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Saliba, Bonnie Colby, David B. Bush, and William E. Martin. Water marketing in the Southwest—Can market prices be used to evaluate water supply augmentation projects? USDA Forest Service General Technical Report RM-144, 44 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

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Southwest



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General Technical
Report RM-145

Forest Habitat Types in the Apache, Gila, and Part of the Cibola National Forests, Arizona and New Mexico

E. Lee Fitzhugh,
William H. Moir,
John A. Ludwig,
and
Frank Ronco, Jr.



Forest Habitat Types in the Apache, Gila, and Part of the Cibola National Forests, Arizona and New Mexico

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Abstract

A habitat type classification is described for forests in the mountains of the Apache, Gila, and Cibola (Magdalena District only) National Forests in Arizona and New Mexico. Using methods modified from those originally developed by Rexford Daubenmire, 7 series, including 40 habitat types and one community type were identified. Descriptions of the habitat types, management implications, association tables, and a key to the types are presented.

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Forest Habitat Types in the Apache, Gila, and Part of the Cibola National Forests, Arizona and New Mexico

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INTRODUCTION

Rexford Daubenmire introduced and developed the habitat type system of ecological classification in the western United States (Daubenmire 1952, Daubenmire and Daubenmire 1968) to provide homogeneous ecological categories for information storage and retrieval, and for predictive capability (Layser 1974, Daubenmire 1976, Pfister 1981). Daubenmire's method defined areas of the land surface which supported similar and recurring patterns of vegetation in an undisturbed state and were considered to have equivalent ecological responses and potential. Several ecologists have further developed and applied the system, modifying the field techniques for greater efficiency and in some cases modifying the classification methods to better fit the needs of practicing foresters. Notable among early publications is Franklin et al. (1970). Probably the most extensive application of the system to date is the work of Robert D. Pfister, who supervised classification of all the timbered National Forest land in Montana (Pfister et al. 1977). Similar work has been done or is still in progress in all 11 western states except, to the best of our knowledge, Nevada.

In 1973, William H. Moir began classifying the spruce-fir and mixed conifer vegetation of Arizona and New Mexico (Moir and Ludwig 1979). This was a broad reconnaissance to identify the major habitat types of high elevation forests—true firs and spruces (*Abies* and *Picea*)—in the two states. In 1974, work began on a classification of the *Pinus ponderosa* forests of northern Arizona (Hanks et al. 1983). Their classification included only four National Forests, and was partially intended as a test to determine whether the Daubenmire system was practical where disturbance and slow recovery were typical. Remnant stands were found for classification purposes in most areas. Some communities had to be identified as “community types,” indicating that the potential of those types was unknown.

In order to provide continuity between these early studies and future ones, a study plan was prepared for classifying coniferous vegetation of all the National Forests in New Mexico, southern Colorado, and Arizona⁴. Ecologically and climatologically similar administrative areas were grouped for the purpose of collecting and

analyzing data. This report presents a classification initiated under that study plan.

The present authors and others associated with them have completed similar studies in the remaining mountain ranges of Arizona, southern Colorado, and New Mexico. Therefore, identification of habitat types and names has been carefully integrated. Results of these studies also are correlated⁵ with the Terrestrial Ecosystem Survey (USDA Forest Service 1983) used in the Southwest Region of the United States Forest Service.

Habitat types identified in this and similar research correspond to the association level defined by the digitized ecosystem classification (Brown et al. 1980) and the “first approximation” of Hall (1984). Revisions of this classification are anticipated as an ongoing process as the system becomes more widely used. This classification is compatible with the national land classification system (Driscoll et al. 1983). Habitat types as used here are at the same level of classification as the “associations” defined by Forest Service Manual 2060, “Ecosystem Classification, Interpretation, and Application.” The difference is that “habitat type” refers to all stands having the same potential, regardless of present seral condition, while “association” refers to an actual stand near the climax condition.

STUDY AREA

This classification includes the forested areas of the Apache National Forest (Arizona and New Mexico), the Gila National Forest (New Mexico), and the Magdalena District of the Cibola National Forest (New Mexico) (fig. 1). The Magdalena District is more similar to the Gila National Forest in plant geography, ecology, and climate than to the remainder of the Cibola National Forest. The Magdalena District is in the upper Gila Mountains Forest Province in Bailey's (1980) classification. Other timbered parts of the Cibola National Forest are in the Rocky Mountain Forest Province and are separated from the Magdalena District by a broad stretch of grassy plains and grassy or juniper-covered mountains (Bailey's Colorado Plateau Province).

The study area encompasses the southeastern end of the Mogollon Rim, a large uplifted escarpment that ex-

⁴Ronco, Frank, Jr., William H. Moir, and E. Lee Fitzhugh. 1978. Study Plan FS#1203.78: Forest habitat type classification for Arizona, New Mexico, and southwestern Colorado. On file at the Forestry Sciences Laboratory, Rocky Mountain Forest and Range Experiment Station, Flagstaff, Ariz.

⁵Report of Working Group No. 4, Habitat Types and the Terrestrial Ecosystem Survey. p. 106-107. In *Proceedings of the Workshop on Southwestern Habitat Types*. April 6-8, 1983, Albuquerque, NM. Technical coordinators, W. H. Moir and Leonard Hendzel. 1983 USDA, Forest Service, Southwestern Region.

tends north and west to northwestern Arizona. Other mountain ranges include the White and Big Lue Mountains and the Blue Range in Arizona; and in New Mexico, the San Francisco, Saliz, Tularosa, Gallo, Mangas, Mimbres, Magdalena, and San Mateo Mountains and the Black Range. Several of the mountain ranges include peaks rising above 10,000 feet (3,048 m). The Big Burro Mountains and the Pinos Altos Range in New Mexico were excluded from the study. Geological origins of the high mountains in the study area are volcanic with various kinds of igneous rocks in different parts of the area.

Moist air from the Gulf of Mexico and violent convective summer storms dominate the climate of the area. The study area forms the southeastern end of the Upper Gila Mountains Forest Province (Bailey 1980). It borders the Mexican Highlands Shrub Steppe Province, the Grama-Tobosa Section of the Chihuahuan Desert Province, and the Grama-Galleta Steppe + Juniper-Pinyon Woodland Mosaic Section of the Colorado Plateau Province. Therefore, the study area is at the confluence of four provinces and two divisions (Desert and Steppe) in Bailey's classification which, at these levels, is primarily climatological. Plants typical of all of these provinces are found in the study area, particularly at lower elevations. The study area seems to be in a region of rapid change in plant ecological relationships, and some plants appeared to have different ecological niches than reported by Hanks et al. (1983), DeVelice et al. (1986), and others. The study area is located at the apex of a "V" formed by the convergence of the eastern terminus of the Mogollon Rim of Arizona with the Continental Divide of the Rocky Mountains. The most rapid ecological change appears to occur from eastern Arizona through southern New Mexico.



Figure 1.—Location of the National Forests included in the habitat type classification study (only the Magdalena District of the Cibola was classified).

CLASSIFICATION THEORY AND NOMENCLATURE

The situation described above represents a geographical gradient, but communities are recognizable, occur with enough frequency to allow recognition, and can be classified into habitat types and phases. Thus, the relationships between gradient theory and community theory are observable in the broad geographical gradients of vegetation throughout the study area, as influenced by extensive and gradual changes in site factors. The gradients are separable into discrete associations influenced by abrupt changes in site factors. Classification is an abstraction for the convenience of users. Each approach has its unique characteristics and utility, and we have chosen the more compartmentalized approach to facilitate mapping, field identification, and information storage for management use. The types are first conceptualized as recognizable plant assemblages which are duplicated on similar sites. Following recognition, names are chosen to facilitate communication.

The foregoing discussion illustrates two additional important concepts that users should consider: (1) naming types is a process distinct from defining them, and (2) disagreement with a name or what it may connote to different individuals should not automatically raise questions about validity of the type definitions.

METHODS

Sampling

Field methods in this classification follow an earlier study plan.⁴ They are similar to those described in Moir and Ludwig (1979, 1983), Pfister and Arno (1980), and Hanks et al. (1983). All of these relied on Daubenmire's (1952) methods. A reconnaissance method was used in which all environmentally and vegetationally different areas were sampled. Circular plots 0.093 acre (375 m²) were subjectively located to ensure environmental homogeneity within the plot. Where vegetation patchiness was of small enough scale, plots included both patch and gap phases of the mosaic. Numerous physical site characteristics were recorded, including slope, aspect, elevation, parent rock, and soil depth and texture. We also recorded crown cover for shrub and herb species, and stem diameter class for tree species. Stem counts by size class provided a better approximation of the ecological role of trees than did canopy cover.

Types previously identified by Moir and Ludwig (1979) or Hanks et al. (1983) were sampled only enough to document their existence. Some plot data from their work were analyzed as part of this study when the plots occurred within the study area.

Data Analysis

We used successive approximations to classify stands as described by Pfister and Arno (1980), Moir and Ludwig (1983), DeVelice et al. (1986), and others. Several dif-

ferent approaches toward classification were tried, including: (1) grouping by dominance according to strata, (2) site factors, (3) presence or consistency of plant unions, (4) presence of any one of several species having approximately similar patterns of occurrence with respect to site factors, and (5) patterns observed in ordinations (Orloci 1966).

We carefully examined site characteristics within groups in the intermediate classifications, identifying those plots with nonconforming environments. We used mathematical ordinations to judge and illustrate quantitative consistency within and between types.

We compared our classification with others previously published (Moir and Ludwig 1979), or in various stages of completion at that time (Hanks et al. 1983; Alexander et al. 1984a, 1984b, 1986; DeVelice et al. 1986). We reconciled differences between classifications in order to provide the most logical units with respect to local and regional patterns. Thus, changes from type descriptions and nomenclature presented by Moir and Ludwig (1979) and Hanks et al. (1983) should be viewed as refinement of previous work based on addition of more data. Changes usually involved small differences in definition and some shifting of their plots from one type to another. When deemed advisable to prevent confusion, we assigned a new name.

Twenty-four of the 55 habitat types, phases, and community types in Appendix D are represented by 4 or fewer plots each, but only 5 of the 24 may be considered undersampled types. Fourteen are habitat types or phases described by the authors cited above. The existence of these 14 habitat types in the present study area was established by a few plots in order to reduce cost. Although we could not describe the full range of variability of these types within the study area, one or more of the above studies adequately covered such variability. In 10 cases, the other study included all or part of the present study area, as well as other locations.

Of the remaining 10 subdivisions having small sample sizes, 5 are unique but uncommon phases of more widespread habitat types, and 5 are separate, unique habitat types encountered too infrequently to sample adequately. We considered these types to be sufficiently distinct and to exhibit such a potential importance for management to identify them at this time.

Compensating factors often caused one type to occur on different slopes, aspects, or elevations. We did not subdivide such types unless there was an obvious difference in the plant community. Such subdivisions, including soils information, would increase specificity of the types for management application, and generally are accomplished by the Terrestrial Ecosystems Surveys (U.S. Forest Service 1983).

Successional stages of habitat types require more study before they can be identified, but successional trends that we observed are noted in this publication.

Naming the Types

New habitat types were named based on diagnostic characteristics. Those species with high fidelity or high

mean abundance within a habitat type were chosen for the nomenclature of a habitat type. Whenever possible, habitat type names and keys utilized the names of plant species that were ecologically significant. However, this procedure was not always practical. Therefore, while some degree of importance can be attached to plants identified in the names and keys, they should not be considered the only ones of importance, or even the most important. Indeed, plants identified in the name of a type may occasionally be absent from some sites representative of the type. A list of all plants identified in the study is shown in appendix B.

There appears to be a gradient of growth form, stand characteristics, and fire response in *Quercus gambelii* from west to east along the "V" previously mentioned from northwestern Arizona to the Gila National Forest and up through the Rocky Mountains. We recognized this gradient between habitat types in the Rocky Mountains and Arizona in separating some habitat types. For example, the Rocky Mountain *Pinus ponderosa*/*Quercus gambelii* habitat type (DeVelice et al. 1986) is found in a broad geographical area northward and eastward from our study area. Hanks et al. (1983), however, used *Quercus gambelii* in Arizona to identify phases of several *Pinus ponderosa* habitat types. Their approach appears to be equally well-founded, and the resulting plant associations may be found over a large area northwestward from the present study.

In this study, it seemed appropriate to retain the nomenclature procedure of Hanks et al. (1983), using *Quercus gambelii* to identify phases, as well as having the species designate a habitat type as is appropriate in the southern Rocky Mountains (DeVelice et al. 1986). The treatment of *Quercus gambelii* is exemplary of other species as well, and illustrates the transitional nature of the study area. Large areas adjacent to the Gila National Forest contain distinctly different *Quercus gambelii* ecotypes, which happen to merge in the Gila National Forest. Distinguishing transitional habitat types identified in this study from those that are typically found in the southern Rocky Mountains and Arizona was somewhat arbitrary. For example, one grouping was named with *Quercus gambelii* as a habitat type descriptor, while its neighbor in the transition zone was named with *Quercus gambelii* as a phase descriptor.

We followed Hanks et al. (1983) in naming the *Pinus ponderosa*/*Arctostaphylos pungens* community type (c.t.). The PIPO/ARPU c.t. is a fire disclimax, at least within our study area, and does not warrant habitat type status.

Users of this classification should reference Lehr (1978), Weber and Johnson (1979), Martin and Hutchins (1980), or Lehr and Pinkava (1980, 1982) to identify their plant specimens. We used the name favored by the majority of the above references, listing other names as synonyms (Appendix B). When all three authors classified plants differently, we used Martin and Hutchins (1980) as reference. In a few instances, synonymy was confirmed by the National List of Scientific Plant Names (USDA 1982a, 1982b). In the few situations where we did not distinguish between two closely related species, the name of the more widespread one was used. We used

Carex foenea to designate and include other rhizomatous species, such as *C. praegracilis*, that are difficult to distinguish. Similarly, we grouped the shorter caespitose sedges as *Carex rossii* and included *Pinus discolor* with *Pinus edulis*. Nickerson et al. (1976) was the authority for common names.

DESCRIPTIONS OF HABITAT TYPES

The following descriptions provide characteristic features for each habitat type and phase identified in the study (table 1), with some tentative management implications. The descriptions should be sufficient, in most cases, to confirm the habitat type that was derived from the keys shown in Appendix A. When descriptions contain too little information to confirm doubtful stands, reference to the successional status of trees (Appendix C) and to the summary association tables (Appendix D) may be helpful. Descriptions are arranged according to series and habitat type. Local topography, microclimate, and soil moisture relationships often cause reversal of the normal elevational order (fig. 2), even at the series level.

Picea engelmannii Series

Picea engelmannii/Moss habitat type (PIEN/Moss; Engelmann spruce/moss)

This type was found at the summit of Black Mountain (Mogollon Mountains, Gila National Forest) and in the San Mateo Mountains, Cibola National Forest.

Vegetation.—*Picea engelmannii* is the dominant tree, with *Pseudotsuga menziesii* sometimes important as a seral tree. Seral or minor trees may include *Abies concolor* and *Pinus strobiformis*. Undergrowths are characteristically sparse, even in small openings and under relatively open canopies. *Vaccinium* spp., if present, provide less than 2% cover. Herbs are infrequent. Lichens and mosses are abundant at microsites that are not covered by deep, extensive litter.

Physical setting.—We found this type on summits, ridgetops, and dry, upper slopes subject to deep persistent snowpacks (fig. 3). Elevations in the San Mateo Mountains are 9,500–10,000 feet (2,896–3,048 m), with cryic soil temperatures.

Adjacent habitat types.⁶—The PIEN/Moss HT usually is bordered by the ABLA/VAMY HT on more sheltered or wetter sites, by the PSME/FEAR HT on ridgetops, and by the ABCO/ACGL HT on lower slopes.

Discussion.—In our study area this habitat type apparently is found only within established wilderness areas. Our late seral plots varied from those described by Moir and Ludwig (1979) in the codominance of *Pseudotsuga menziesii* and absence of *Abies lasiocarpa*. Seral stages include abundant *Acer glabrum* and *Jamesia americana* in the undergrowth. Postdisturbance succes-

⁶Only the major, commonly observed relationships are described in this publication.

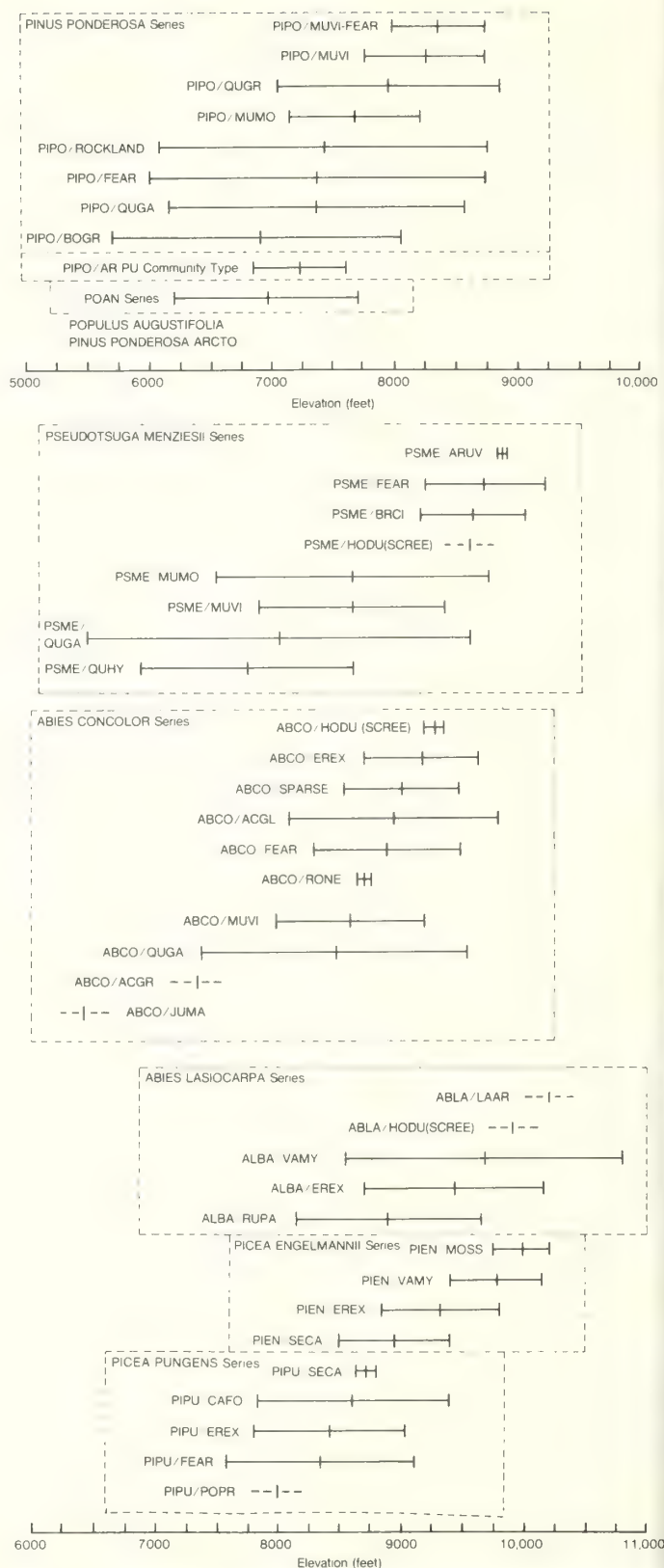


Figure 2.—General elevational relationship of forest habitat types in the study area. (The upper and lower elevations for each type are data from individual sample plots, respectively; the midpoint of the elevational range is denoted by a vertical bar, except for habitat types sampled by a single plot, where the unknown range is indicated by a dotted line and one bar is the plot elevation.)

Table 1.—List of habitat types and plant communities identified on the Apache, Gila, and part of the Cibola National Forests

Habitat Type Name	Abbreviation
<i>Picea engelmannii</i> Series	
<i>Picea engelmannii</i> /Moss habitat type	PIEN/Moss HT
<i>Picea engelmannii</i> /Vaccinium myrtillus habitat type	PIEN/VAMY HT
<i>Picea engelmannii</i> /Senecio cardamine habitat type	PIEN/SECA HT
<i>Abies lasiocarpa</i> phase	ABLA phase
<i>Abies concolor</i> phase	ABCO phase
<i>Picea engelmannii</i> /Erigeron eximius habitat type	PIEN/EREX HT
<i>Abies lasiocarpa</i> Series	
<i>Abies lasiocarpa</i> /Vaccinium myrtillus habitat type	ABLA/VAMY HT
<i>Vaccinium myrtillus</i> (typic) phase	VAMY (typic) phase
<i>Rubus parviflorus</i> phase	RUPA phase
<i>Abies lasiocarpa</i> /Lathyrus arizonicus habitat type	ABLA/LAAR HT
<i>Abies lasiocarpa</i> /Holodiscus dumosus (Scree) habitat type	ABLA/HODU (Scree) HT
<i>Abies lasiocarpa</i> /Erigeron eximius habitat type	ABLA/EREX HT
<i>Abies lasiocarpa</i> /Rubus parviflorus habitat type	ABLA/RUPA HT
<i>Picea pungens</i> Series	
<i>Picea pungens</i> /Senecio cardamine habitat type	PIPU/SECA HT
<i>Picea pungens</i> /Erigeron eximius habitat type	PIPU/EREX HT
<i>Picea pungens</i> /Carex foenea habitat type	PIPU/CAFO HT
<i>Picea pungens</i> /Festuca arizonica habitat type	PIPU/FEAR HT
<i>Picea pungens</i> /Poa pratensis habitat type	PIPU/POPR HT
<i>Abies concolor</i> Series	
<i>Abies concolor</i> /Erigeron eximius habitat type	ABCO/EREX HT
<i>Abies concolor</i> (Sparse) habitat type	ABCO/Sparse HT
<i>Abies concolor</i> /Holodiscus dumosus (Scree) habitat type	ABCO/HODU (Scree) HT
<i>Abies concolor</i> /Acer glabrum habitat type	ABCO/ACGL HT
<i>Abies concolor</i> /Muhlenbergia virescens habitat type	ABCO/MUVI HT
<i>Abies concolor</i> /Quercus gambelii habitat type	ABCO/QUGA HT
<i>Quercus gambelii</i> (typic) phase	QUGA (typic) phase
<i>Muhlenbergia virescens</i> phase	MUVI p.
<i>Abies concolor</i> /Robinia neomexicana habitat type	ABCO/RONE HT
<i>Abies concolor</i> /Festuca arizonica habitat type	ABCO/FEAR HT
<i>Festuca arizonica</i> (typic) phase	FEAR (typic) phase
<i>Poa fendleriana</i> phase	POFE p.
<i>Abies concolor</i> /Acer grandidentatum habitat type	ABCO/ACGR HT
<i>Abies concolor</i> /Juglans major habitat type	ABCO/JUMA HT
<i>Pseudotsuga menziesii</i> Series	
<i>Pseudotsuga menziesii</i> /Arctostaphylos uva-ursi habitat type	PSME/ARUV HT
<i>Pseudotsuga menziesii</i> /Holodiscus dumosus (Scree) habitat type	PSME/HODU (Scree) HT
<i>Pseudotsuga menziesii</i> /Festuca arizonica habitat type	PSME/FEAR HT
<i>Pseudotsuga menziesii</i> /Bromus ciliatus habitat type	PSME/BRCI HT
<i>Pseudotsuga menziesii</i> /Quercus gambelii habitat type	PSME/QUGA HT
<i>Quercus gambelii</i> (typic) phase	QUGA (typic) phase
<i>Muhlenbergia virescens</i> phase	MUVI phase
<i>Festuca arizonica</i> phase	FEAR phase
<i>Pseudotsuga menziesii</i> /Muhlenbergia virescens habitat type	PSME/MUVI HT
<i>Pseudotsuga menziesii</i> /Muhlenbergia montana habitat type	PSME/MUMO HT
<i>Pseudotsuga menziesii</i> /Quercus hypoleucoides habitat type	PSME/QUHY HT
<i>Pinus ponderosa</i> Series	
<i>Pinus ponderosa</i> /Muhlenbergia virescens habitat type	PIPO/MUVI HT
<i>Muhlenbergia virescens</i> (typic) phase	MUVI (typic) phase
<i>Quercus gambelii</i> phase	QUGA phase
<i>Pinus ponderosa</i> /Muhlenbergia virescens-Festuca arizonica habitat type	PIPO/MUVI-FEAR HT
<i>Muhlenbergia virescens-Festuca arizonica</i> (typic) phase	MUVI-FEAR (typic) phase
<i>Quercus gambelii</i> phase	QUGA phase
<i>Bouteloua gracilis</i> phase	BOGR phase
<i>Pinus ponderosa</i> /Quercus grisea habitat type	PIPO/QUGR HT
<i>Muhlenbergia montana</i> phase	MUMO phase
<i>Muhlenbergia longiligula</i> phase	MULO phase
<i>Pinus ponderosa</i> /Rockland habitat type	PIPO/Rockland HT
<i>Pinus ponderosa</i> /Festuca arizonica habitat type	PIPO/FEAR HT
<i>Festuca arizonica</i> (typic) phase	FEAR (typic) phase
<i>Quercus gambelii</i> phase	QUGA phase
<i>Bouteloua gracilis</i> phase	BOGR phase
<i>Pinus ponderosa</i> /Muhlenbergia montana habitat type	PIPO/MUMO HT
<i>Pinus ponderosa</i> /Quercus gambelii habitat type	PIPO/QUGA HT
<i>Quercus gambelii</i> (typic) phase	QUGA (typic) phase
<i>Muhlenbergia longiligula</i> phase	MULO phase
<i>Pinus ponderosa</i> /Bouteloua gracilis habitat type	PIPO/BOGR HT
<i>Pinus edulis</i> phase	PIED phase
<i>Vitis arizonica</i> phase	VIAR phase
<i>Pinus ponderosa</i> /Arctostaphylos pungens Community Type	PIPO/ARPU CT
<i>Populus angustifolia</i> series	POAN series

sion begins with a *Populus tremuloides*/*Pseudotsuga menziesii* community, converting to a stand containing only *Pseudotsuga menziesii*, and then to the late seral mixed codominance stage. The type represents poor site quality for *Pseudotsuga menziesii*.

***Picea engelmannii*/Vaccinium myrtillus habitat type (PIEN/VAMY; Engelmann spruce/Rocky Mountain whortleberry)**

We found the PIEN/VAMY HT in the San Mateo Mountains, Magdalena Ranger District, Cibola National Forest.

Vegetation.—The PIEN/VAMY HT may be recognized by the absence of *Abies lasiocarpa* and the strong competitive presence of *Picea engelmannii*—which in our plots totaled at least 170 stems per acre in the regeneration class.⁷ *Pseudotsuga menziesii* was present, and sometimes even dominated seral stands. *P. menziesii* regeneration occurs, but was much less vigorous than that of *Picea engelmannii*.

The undergrowth was dominated by a low shrub layer always containing *Vaccinium myrtillus* (fig. 4), with *Lonicera utahensis*, *Physocarpus monogynus*, and *Ribes pinetorum* often present. The tall shrubs, *Acer glabrum*, *Jamnesia americana*, and *Salix scouleriana* often were present.

Herbaceous vegetation was sparse, with few species having more than 1% coverage. Species often present included: *Bromus ciliatus*, *Goodyera repens*, *Erigeron eximius*, *Pyrola chlorantha*, and *Ramischia secunda*.

The PIEN/VAMY HT differs from the ABLA/VAMY HT in the absence of *Abies lasiocarpa*, the relatively sparse (30% or less) coverage of *Vaccinium myrtillus*, and greater seral importance of *Pseudotsuga menziesii*.

Physical setting.—The PIEN/VAMY HT occurs on cold sites where snow persists late into the spring, but the sites may be drier and warmer than in the ALBA/

⁷Regeneration and reproduction are used synonymously to denote trees that are less than 4.5 feet (1.37 m) tall.



Figure 3.—*Picea engelmannii*/Moss habitat type. Teepee Peak, San Mateo Mountains, 9,970 feet (3,038 m) elevation. Upper slope and ridgetop sites with deep, persistent snowpack support an undergrowth dominated by moss, lichen, and litter.



Figure 4.—*Picea engelmannii*/Vaccinium myrtillus habitat type. Cub Spring, San Mateo Mountains, 9,400 feet (2,865 m) elevation. *Picea engelmannii* and shrubs dominate, with *Vaccinium myrtillus* prominent.

VAMY HT. We found the PIEN/VAMY HT from 9,400 to 10,150 feet (2,865 to 3,093 m) elevation on north and northeast slopes with gradients of 30% to 60%. It was on upper slopes except at the lowest elevation, where it was found in a draw. Soils were very cobbly.

Adjacent habitat types.—Ridgetops support the PIEN/MOSS or PSME/FEAR HT's. Cobble-scrub soils below the PIEN/VAMY HT support the ABCO/ACGL HT. On warmer sites the PIEN/VAMY HT adjoins mixed conifer habitat types.

Discussion.—Several authors working in the Southwest and elsewhere have described habitat types involving various combinations of *Picea engelmannii*, *Abies lasiocarpa*, *Vaccinium myrtillus*, *Vaccinium scoparium* (VASC), and *Polemonium pulcherrimum* (POPU) or *Polemonium delicatum* (PODE) (Moir and Ludwig 1979, Youngblood and Mauk 1985, Alexander et al. 1986, DeVelice et al. 1986, and others). Our PIEN/VAMY HT appears more closely related in site characteristics and floristics to habitat types in the *Abies lasiocarpa* series, with a *Vaccinium myrtillus* or *V. scoparium* undergrowth, than to the near-tundra PIEN/VAMY/POPU HT of DeVelice (1986). However, one of our plots was reminis-

cent of the latter type, as described by Moir and Ludwig (1979) under the name PIEN/VASC/PODE. Our PIEN/VAMY HT differs from the above types in that it lacks *Abies lasiocarpa* and has less herbaceous and low shrub cover.

Crown fires result in successional stages dominated by *Populus tremuloides* and a dense herbaceous layer. The cold, snowy sites limit timber management opportunities, but proper harvesting and grazing techniques can increase water production and quality.

***Picea engelmannii*/Senecio cardamine habitat type (PIEN/SECA; Engelmann spruce/cardamine groundsel)**

We found this type only in the vicinity of Hannagan and Thomas Creek drainages, Blue Mountains, Apache National Forest, and Bearwallow Mountain, Mogollon Mountains, Gila National Forest.

Vegetation.—The overstory is a mixture of *Pseudotsuga menziesii* and *Picea engelmannii*, frequently with *Picea pungens*, *Abies concolor*, *A. lasiocarpa*, *Pinus strobiformis*, and *Populus tremuloides*. Tree regeneration is mostly *Picea engelmannii* and/or *Abies lasiocarpa* or *A. concolor*. The combined number of stems less than 10 inches (25.4 cm) d.b.h. of *Picea engelmannii* and *Abies lasiocarpa* usually exceeds that of combined *Abies concolor* and *Pseudotsuga menziesii* by a ratio greater than about 2:1 in most stands.

The undergrowth is characteristically herbaceous often with conspicuous patches of *Senecio cardamine* (fig. 5). Other common herbs include *Pteridium aquilinum*, *Dugaldia hoopesii*, *Viola canadensis*, *Senecio wootoni*, *Geranium richardsonii*, *Fragaria ovalis*, *Bromus ciliatus*, *Erigeron eximius*, *Ramischia secunda*, and *Pyrola chlorantha*.

Shrubs are minor; the most constant species are *Lonicera utahensis* and *Rubus parviflorus*.

Moir and Ludwig (1979) described two phases. When *Abies lasiocarpa* has light to moderate regeneration, it is used as the phase name. When it is absent or sparse and *A. concolor* has light to moderate regeneration, the



Figure 5.—*Picea engelmannii*/Senecio cardamine habitat type. Turkey Creek drainage, Mogollon Mountains, 9,400 feet (2,865 m) elevation. Undergrowth typically herbaceous, often with conspicuous patches of *Senecio cardamine* or the low shrub, *Pachistima myrsinites*.

latter species designates the phase. *Pachistima myrsinites* often is found in the *Abies concolor* phase, while *Lonicera utahensis* is present in both phases but is found less often in the *Abies concolor* phase. Other shrubs may be present. *Mertensia franciscana* and *Fragaria americana* are sometimes present in the *Abies concolor* phase but are absent in the *Abies lasiocarpa* phase.

Physical setting.—Mean annual precipitation is about 29 inches (74 cm) (Beschta 1976). Elevations range from 8,500 to 9,400 feet (2,590 to 2,865 m) mostly on gentle slopes. The *Abies lasiocarpa* phase occurs on north and east aspects mostly at 9,000 feet (2,743 m) and above, often on upper slopes and ridges, and the *Abies concolor* phase tends to be found on slightly warmer northerly aspects, steeper slopes, and lower positions on the slope. According to the Terrestrial Ecosystem Survey, the soils are of basaltic origin, moderately deep to deep, and with a fine-loamy or loamy-skeletal texture (U.S. Forest Service 1983). They are classed as mixed, Mollic Cryoboralfs near the warm margin of the cryic soil temperature regime.

Adjacent habitat types.—Habitat types at lower elevations are ABCO/QUGA, ABCO/Sparse, and PIPU/FROV. Stands intergrading with the PIPU/SECA HT can be found. At higher elevations, the ABLA/EREX HT may adjoin this type.

Discussion.—Streamside sites in the *Abies concolor* phase could be separated into another phase having more mesic forbs, but there were too few plots for good definition. Although geographically limited, the PIEN/SECA HT has close environmental and floristic relationships to other habitat types that display essentially herb-rich undergrowths at the low elevation, warm border of the spruce-fir region. These include the ABLA/VAMY, RUPA phase, ABLA/EREX, and PIPU/EREX HT's.

Cessation of fires in the last 50 years is evident by increased numbers of shade tolerant *Picea engelmannii* and *Abies lasiocarpa* in the undergrowth. Generally this habitat type has a fire history characterized by frequent, low intensity fires as well as larger, more intense, surface fires at a mean interval of about 22 years (Dieterich 1983). However, our sites were undisturbed by fire within the past 50 years. Centuries of such fire history help explain the mixtures of such seral species as *Populus tremuloides*, *Pinus ponderosa*, *P. strobiformis*, and *Pteridium aquilinum*.

The PIEN/SECA HT is found on sites that are of high quality for tree growth. However, windthrow could be a problem following logging, as indicated by its natural occurrence in undisturbed stands. Five-year growth and development was studied by Gottfried (1978) in an undisturbed, old-growth stand within this habitat type. The abundance of forbs in this type indicates greater utility for sheep or deer forage than for cattle. The PIEN/SECA HT is esthetically important because of the variety of species present at relatively low, accessible locations.

***Picea engelmannii*/Erigeron eximius habitat type (PIEN/EREX; Engelmann spruce/forest fleabane)**

The PIEN/EREX HT (fig. 6) is widely distributed throughout the study area. Our plots were along the Mim-

bres River, and in the Black Range, Mogollon Mountains, and White Mountains of the Apache and Gila National Forests. The Springerville, Alpine, Reserve, Glenwood, and Mimbres Ranger Districts were represented.

Vegetation.—*Picea engelmannii* and/or *Pseudotsuga menziesii* are climax dominants. *Abies concolor* and *Pinus strobiformis* are minor climax and seral trees respectively, which are sometimes abundant as reproduction, but never in the larger size classes. *Populus tremuloides* is a major seral species. *Abies lasiocarpa* and *Pinus ponderosa* are accidental in mature stands, the former occurring only as reproduction. *P. ponderosa* is an early seral tree in this habitat type, occurring as an occasional mature tree in some stands.

Stands lacking *Picea pungens* may have less than 14% graminoid cover, less than 30% forb cover, and less than 45% total herbaceous cover. On more gentle slopes, *Erigeron eximius* increases to 20% cover. Where *Picea pungens* is a minor climax tree, herbaceous cover is greater in all three categories.

Shrubs are unimportant, having less than 7% cover in our plots. *Rubus parviflorus* often is present.

Graminoids usually have less coverage than do forbs, and in our plots graminoid coverage ranged from 7% to 52%. *Bromus ciliatus* and *Carex foenea* were dominants, with the former always present. Both caespitose and rhizomatous sedges usually were present.

Forbs covered 19–102% of the area (higher coverage represents overlapping layers). *Geranium richardsonii* and *Lathyrus arizonicus* always were present. These two



Figure 6.—*Picea engelmannii*/*Erigeron eximius* habitat type. Quaking Aspen Creek, Mogollon Mountains, 9,040 feet (2,755 m) elevation. *Picea engelmannii*, *Pseudotsuga menziesii*, and grasses or forbs characterize these sites at the lower edge of *Picea engelmannii*-*Abies lasiocarpa* forests.

were dominant in some plots as were *Erigeron eximius*, *Senecio bigelovii*, *Smilacina stellata*, and *Thalictrum fendleri*. Other plants frequently present included *Fragaria ovalis*, *Haplopappus parryi*, *Ligusticum porteri*, *Osmorhiza depauperata*, *Pseudocymopterus montanus*, *Vicia americana*, and *Viola canadensis*.

Physical setting.—The PIEN/EREX HT occurs from 8,850 to 9,800 feet (2,697 to 2,987 m) elevation at the lower, warmer zone of the *Picea engelmannii* elevational range. *Picea pungens* occurs throughout the entire elevational range of the habitat type, on all aspects, and with slopes varying from 7% to 50%. Stands without *Picea pungens* occur mostly on northeast exposures of steep middle to lower slopes (28–50%) above 9,000 feet (2,743 m).

Adjacent habitat types.—Moister sites in the White Mountains support the PIEN/SECA HT, while the PSME/BRCI HT sometimes is intermixed with the PIEN/EREX HT. Stands at lower and drier sites are composed of ABCO/MUVI, PIPU/FEAR, ABCO/Sparse, or PIPU/EREX HT's.

Discussion.—The PIEN/EREX HT includes some plots assigned by Moir and Ludwig (1979) to their *Picea pungens*-*Picea engelmannii*/*Erigeron superbus* habitat type. The remaining plots were assigned to the *Picea pungens*/*Erigeron eximius* habitat type.

Populus tremuloides may be expected to occupy a site following clearcutting, but *Picea engelmannii* regenerates readily under a canopy. Logging resulted in the establishment of *Abies concolor*, *Pteridium aquilinum*, and *Carex foenea*. We noted witches brooms on large *Pseudotsuga menziesii* and *Picea engelmannii*. Elk used the habitat type heavily.

Abies lasiocarpa Series

***Abies lasiocarpa*/Vaccinium myrtillus habitat type (ABLA/VAMY; subalpine fir/Rocky Mountain whortleberry)**

The typical phase was sampled in the White Mountains and on Escudilla Mountain, Apache National Forest, Arizona, and in the Mogollon Mountains, Gila National Forest, New Mexico. The *Rubus parviflorus* phase was sampled in the Mimbres and Mogollon Mountains of the Gila National Forest.

Vegetation.—*Picea engelmannii* and *Abies lasiocarpa* usually are codominant, both producing abundant regeneration. However, in some stands, one of these species can be dominant, the other minor. *Pseudotsuga menziesii* is found occasionally at lower elevations where it can be a seral tree, achieving codominance on individual sites, but with little regeneration evident. *Populus tremuloides* is a common seral tree.

The undergrowth characteristically is dominated by *Vaccinium myrtillus*. Its cover usually exceeds 30%, but may be as low as 2% (fig. 7). Other common shrubs are *Lonicera involucrata*, *L. utahensis*, *Ribes wolfii*, and *Sorbus dumosa*.

Herbs have less coverage than shrubs, but common species include *Bromus ciliatus*, *Epilobium angustifolium*,

Erigeron eximius, *Fragaria ovalis*, *Haplopappus parryi*, *Luzula parviflora*, *Moneses uniflora*, *Pedicularis angustifolia*, *P. racemosa*, and *Ramischia secunda*.

In the *Rubus parviflorus* phase, *Pseudotsuga menziesii* and *Abies concolor* are seral and may have some regeneration potential, but the relatively few individuals are vastly exceeded by the regeneration densities of the two climax species. *Pinus strobiformis* is found occasionally. There is a well developed shrub assemblage in the *Rubus parviflorus* phase in which *Vaccinium myrtillus* usually is dominant and *Rubus parviflorus* usually exceeds 5% cover. Herbaceous cover is luxuriant (averaging 15–20%) and well represented by such species as *Artemisia franserioides*, *Epilobium angustifolium*, *Erigeron eximius*, *Geranium richardsonii*, *Haplopappus parryi*, *Ramischia secunda*, *Swertia radiata*, and *Viola canadensis*.

Physical setting.—The ABLA/VAMY HT, VAMY phase is found on all slopes and aspects above 9,500 feet (2,896 m) elevation. Stands in the White Mountains are found within the mean annual precipitation isohyets of 30–35 inches (76–89 cm) (Beschta 1976). The ABLA/VAMY HT is part of a circumboreal family of subalpine-subpolar forests (taiga) characterized by deep snowpack and brief, cool summers. Snow course data for 17 years of record from two stations between 10,500 and 10,800 feet (3,200 and 3,292 m) in the Mogollon Mountains reveal mean snow depths of 37–51 inches (94–130 cm) by around February 1, increasing to 47–72 inches (119–183 cm) by around April 1 (Jones 1981). The water

equivalency of this snowpack is about 12 inches (30 cm) in February and 20 inches (51 cm) by April. Greater snow depths and water equivalents are reported between 10,900 and 11,200 feet (3,320 and 3,414 m) in the White Mountains (Jones 1981). These data represent snow conditions in the typic phase, but mostly within forest openings rather than under tree canopies.

Soils can be extremely cobbly or extremely stony, tending toward scree. Soil temperature regimes are toward the colder portions of the cryic spectrum. In the White Mountains, the soils have been described as Dystric Cryochrepts, loamy-skeletal, mixed, cold.⁸

The *Rubus parviflorus* phase commonly is on lower slopes, in draws, or on streamside of northerly exposures around 8,500–9,600 feet (2,591–2,926 m) elevation. It can be found on upper slopes as high as 10,320 feet (3,146 m). Soils specific to the ABLA/VAMY h.t., RUPA phase have not been described, nor are snow course data available. However, the typical phase occurs on cooler sites with deeper snowpack than the *Rubus parviflorus* phase. The soils of the RUPA phase are deep or moderately deep, and sometimes very, or even extremely, cobbly. They are apparently within the warmer portions of the cryic soil temperature spectrum and appear sufficiently moist during the growing season, so that plants, especially the undergrowth, are under little or no moisture stress.

Adjacent habitat types.—On cold, dry ridgetops and upper slopes, the PIEN/MOSS or PSME/FEAR HT's occur adjacent to the ABLA/VAMY HT. However, most ecotones occur in warmer environments and at lower elevations, specifically with the ABCO/ACGL HT (on warm sites with extremely cobbly soils), the ABLA/RUPA HT, and the ABLA/EREX HT. The latter habitat type can also form mosaics, intergrading with stands of the ABLA/VAMY HT. Some of the environmental subtleties that account for these habitat types are unclear. However, some of the relationships are listed below:

Vegetation	Elevation—ft (m)	Position on Slope
ABLA/VAMY HT, VAMY phase	>9,500 (>2,913 m)	Mid and upper
ABLA/EREX HT	8,900–10,200	Upper to lower
ABLA/VAMY HT, RUPA phase	(2,713–3,109 m)	
	8,700–10,320	Upper to lower
ABLA/RUPA HT	(2,651–3,146 m)	
	8,140–9,640	Mid, lower, and stream-side benches
	(2,481–2,938 m)	

Discussion.—Much of this habitat type occurs in the Gila and Baldy Wilderness Areas. The environmental and productive variability of the type has been discussed by Moir and Ludwig (1979) within their *Abies lasiocarpa/Vaccinium scoparium* habitat type (ABLA/VASC HT)—they indicate that timber productivity varies greatly depending on site. One of the most important overall management considerations is the value of this habitat type for snow catchment and water production. The ABLA/VAMY HT is, we believe, the most important of

⁸U.S. Department of Agriculture, Forest Service. 1982. Progress review of Terrestrial Ecosystems Survey of Springerville Ranger District. Unpublished evaluation report (letter July 2, 1982, 2550, including mapping legend).



Figure 7.—*Abies lasiocarpa/Vaccinium myrtillus* habitat type, typic phase. This type, found between 9,560 and 10,800 feet (2,913 and 3,291 m) elevation, is characterized by rich and diverse shrub and forb layers. Site quality for timber varies with aspect and soil type, and is sometimes poor.

all the subalpine types in this region for winter snow accumulation and regulated summer discharge of water. The principles and application of watershed management summarized by Leaf (1975a, 1975b) and Hibbert (1979) seem to apply to the ABLA/VAMY HT.

A ridgetop site in the *Rubus parviflorus* phase in a late successional stage following fire included such species as *Acer glabrum*, *Salix scouleriana*, *Populus tremuloides*, *Holodiscus dumosus*, and abundant *Robinia neomexicana*; *Picea engelmannii* and *Abies lasiocarpa* reproduction and large, mature *Pseudotsuga menziesii*, which survived the fire, also were observed. Ground vegetation was similar to climax, but sparser.

The floristics of this habitat type reveal a strong affinity to other *Vaccinium*-dominated subalpine forests. There is much evidence that during the Pleistocene such forests were more continuous and widespread along the Rocky Mountain Cordillera and through the Basin and Range Physiographic Province. Although these forests are southern geographic outliers, the environment characterizing them is still typically that of the boreal, subalpine forest to which the Cordilleran flora is well adapted. Therefore, relatively few southern or Madrean species are found, the most notable exception being *Pedicularis angustifolia*. The related ABLA/VASC HT described most recently by Mauk and Henderson (1984) is sufficiently different in species composition to be classified as a different habitat type.

Where the *Rubus parviflorus* phase occurs adjacent to streams, *Cornus stolonifera* may dominate at the streamside, and the habitat type may show some affinity to the *Picea pungens*/*Cornus stolonifera* habitat type of Alexander et al. (1986). Youngblood and Mauk (1985) identified an ABLA/VAMY HT in Utah that appears to be similar to our typic phase, as did DeVelice et al. (1986) in northern New Mexico and southern Colorado. The greatest difference between the Utah type and that in New Mexico and Colorado is the absence of *Populus tremuloides* in seral stands in Utah. Perhaps the Utah type of Youngblood and Mauk should be considered a different phase of the habitat type.

The *Rubus parviflorus* phase has similarities to both the ABLA/RUPA and ABLA/EREX HT's. The ages of sampled stands were similar. Gradients exist between these types and the ABLA/VAMY HT, RUPA phase, and the classification divisions among them are somewhat arbitrary. Furthermore, the ABLA/VAMY HT, RUPA phase is related to the extensive *Abies lasiocarpa*/*Vaccinium myrtillus*-*Linnaea borealis* (ABLA/VAMY-LIBO) and *Abies lasiocarpa*/*Vaccinium myrtillus*-*Rubus parviflorus* (ABLA/VAMY-RUPA) habitat types, which are distinct at low elevations in northern New Mexico from the ABLA/VAMY HT (DeVelice et al. 1986). The ABLA/VAMY HT, RUPA phase has less dense forb cover than any of the northern New Mexico types containing *Abies lasiocarpa* and *Vaccinium myrtillus*. It has a closer relationship to the overstory of the ABLA/VAMY-LIBO HT and to the herbaceous layer of the ABLA/VAMY-RUPA HT.

The *Rubus parviflorus* phase mostly occurs within wilderness areas in the National Forests included in this

study. The rich and diverse canopy, shrub, and herbaceous layers make this phase an outstanding habitat for deer, elk, and numerous birds. Because of low grass production compared to forbs, the value for cattle grazing would be limited, but that for sheep would be high.

***Abies lasiocarpa*/Lathyrus arizonicus habitat type (ABLA/LAAR; subalpine fir/Arizona peavine)**

We found this type only on Whitewater Baldy, Mogollon Mountains, Gila National Forest, New Mexico (fig. 8). The type was described by Moir and Ludwig (1979) on the San Francisco Peaks in northern Arizona.

Vegetation.—*Pinus strobiformis* and *Pseudotsuga menziesii* dominate a stand which also contains *Abies lasiocarpa*, and sometimes *Picea engelmannii*. *Abies lasiocarpa* dominates regeneration. Moderate shrub and forb layers are typical, with *Acer glabrum*, *Symphoricarpos oreophilus*, *Lathyrus arizonicus*, and *Vicia americana* dominating.

Physical setting.—This type was inferred from one plot, which was located at 10,200 feet (3,108 m) elevation on a 52%, southeast-facing slope. It was near a mountain crest.

Adjacent habitat types.—This type occurs at the lower edge of the *Picea-Abies* zone and may adjoin stands dominated by *Abies concolor*, *Pseudotsuga menziesii*, *Abies lasiocarpa* or *Picea engelmannii*. It is related to the ABLA/HODU (Scree) HT, but with more soil between cobbles and, consequently, more herbaceous growth.

Discussion.—This type differs from the description of the ABLA/LAAR HT of Moir and Ludwig (1979) in having a lower elevational position relative to other spruce-fir stands and in the dominance of *Pinus strobiformis*. More study is needed to clarify the distinction between the ABLA/LAAR HT and the ABLA/EREX HT at the lower elevational limits of *Abies lasiocarpa*. Fire scars indicated that ground fires are infrequent, but a natural part of this community, and may influence the nature of the herbaceous vegetation.

***Abies lasiocarpa*/Holodiscus dumosus (Scree) habitat type (ABLA/HODU (Scree); subalpine fir/bush rockspirea (scree))**

We found this type on Center Baldy in the Mogollon Mountains, Gila National Forest, but it probably occurs elsewhere in Arizona and New Mexico where site conditions are suitable.

Vegetation.—Our single plot was dominated by *Pseudotsuga menziesii*, with *Pinus strobiformis* and *Abies lasiocarpa* comprising the remainder of the overstory. All three species are climax components. Numerous shrubs were present, with *Symphoricarpos oreophilus*, *Juniperus communis*, and *Holodiscus dumosus* dominant. *Robinia neomexicana* also was conspicuous throughout the stand. Grasses and forbs were relatively minor, but 14 species were present; *Geranium richardsonii* had measurable cover.

Physical setting.—Our plot was at 9,900 feet (3,018 m) elevation on a 54%, south-facing slope. The type extended from the ridgetop to midslope or lower. The critical site factor is the loose rock surface (scree), which limits water storage for shallow-rooted plants (fig. 9).

Adjacent habitat types.—Our plot was adjacent to the ABLA/VAMY HT on the ridge, but the type extended below midslope and presumably contacted more mesic *Abies lasiocarpa* habitat types at lower positions on the slope.



Figure 8.—*Abies lasiocarpa*/*Lathyrus arizonicus* habitat type. This type—found in the Coconino National Forest and Whitewater Baldy, Mogollon Mountains, Gila National Forest—is related to the ABLA/HODU (Scree) HT, but with better soil and more herbaceous growth. The one plot sampled was at 10,200 feet (3,108 m) elevation.

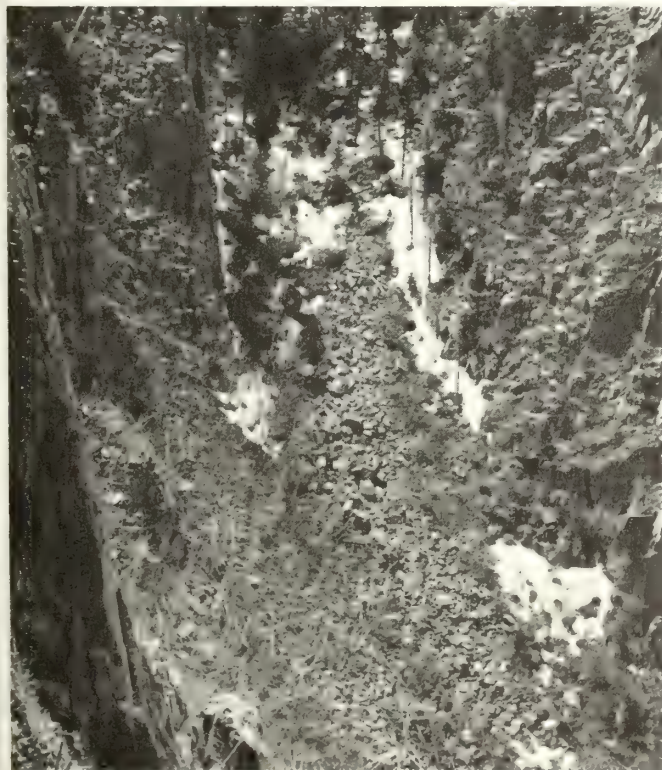


Figure 9.—*Abies lasiocarpa*/*Holodiscus dumosus* (scree) habitat type. Talus from nearby cliffs is the featured soil parent material here. Note down logs from a very recent fire.

Discussion.—The loose rock surface stores solar heat and probably maintains a readily water-absorbent soil underneath, even during winter. Because snow melts more rapidly on the rock surfaces, the scree types are probably important for ground-water recharge. They also are important as rodent and reptile habitats, but not for commercial timber use. The *Abies lasiocarpa*/*Saxifraga bronchialis* habitat type in northern New Mexico (DeVelice et al., 1986) is in a virtually identical environment, although there are some significant differences in vegetation.

***Abies lasiocarpa*/Erigeron eximius habitat type (ABLA/EREX; subalpine fir/forest fleabane)**

This type is widespread and common throughout the study area (fig. 10).

Vegetation.—*Picea engelmannii* and *Abies lasiocarpa* are climax dominants, exhibiting moderate to heavy *Abies lasiocarpa* or *Picea engelmannii* regeneration. *Abies lasiocarpa* regeneration ranges from 70 to 3,400 stems per acre (173 to 8,401 per ha). *Populus tremuloides* is a conspicuous seral tree. *Pseudotsuga menziesii* and *Abies concolor* may be present.

Shrubs cover from 0% to 20% of the area, but usually are a minor component of the community. *Lonicera utahensis* and *Rubus parviflorus* often are present, the latter covering 1% or less of the area. *Vaccinium myrtillus* usually is absent, or has less than 5% cover, much less than herbaceous cover.

The herbaceous undergrowth typically is dense, dominated by forbs with some graminoids, including *Haplopappus parryi*, *Geranium richardsonii*, *Bromus ciliatus*, *Lathyrus arizonicus*, and *Carex foenea*. *Erigeron eximius* is dominant in most stands, usually forming extensive clonal patches. Total forb cover is 10% to more than 100%, usually 20–75%.

Physical setting.—The ABLA/EREX HT is found over a wide range of slopes and aspects between 9,400 and 10,200 feet (2,860 and 3,100 m), and occasionally as low as 8,700 feet (2,651 m). Mean annual precipitation is about 30 inches (76 cm) (Beschta 1976). The forests are somewhat warmer and drier than those of the ABLA/VAMY HT, as indicated by snow course measurements from three stations near the low elevation (between 9,000 and 9,300 feet or 2,743 and 2,835 m) margin of the ABLA/EREX HT (Jones 1981). Data from these stations averaged over at least 13 years, show mean snow depths from both February 1 and April 1 measurement periods to be about 21 inches (53 cm). This is equivalent to about 6 inches (15 cm) of water. The modal environment for the ABLA/EREX HT lies between this minimum limit of winter snowpack and that described for the ABLA/VAMY HT.

Soils occupy the warmer portions of the cryic soil temperature spectrum. They are mostly deep to moderately deep, and vary widely in texture. They have been described in portions of the Springerville Ranger District as Mollic Cryoboralfs, warm, and Argic Cryoborolls, warm.⁸

Adjacent habitat types.—At higher elevations or on colder sites, the ABLA/VAMY and PIEN/BRCI HT's adjoin or form complicated mosaic patterns with the ABLA/EREX HT. Elsewhere, ecotones or mosaics occur mainly with the ABLA/RUPA HT and habitat types containing *Picea pungens* as a climax or coclimax tree. If slope contrasts are strong, then warm south-facing slopes opposite stands of the ABLA/EREX HT may have *Abies concolor* as a major component of the mixed conifer forest.

Discussion.—This habitat type is the *Abies lasiocarpa*/*Erigeron superbus* habitat type (ABLA/ERSU HT) of Moir and Ludwig (1979). The ABLA/EREX HT presents a variety of productive silvicultural opportunities for timber management for *Picea engelmannii* and *Pseudotsuga menziesii*. The diverse and luxuriant undergrowth, combined with thermal protection by the dense overstory, make this an important wildlife habitat for many game and nongame species.

Surface fires probably played the major role in creating mosaics of *Populus tremuloides* and *Pseudotsuga menziesii*, but very little is known about fire succession in this environment (Fischer and Clayton 1983). *Pseudotsuga menziesii* may be maintained in the overstory by periodic ground fires which would selectively remove the more susceptible *Abies* and *Picea* saplings, leaving *P. menziesii*, and providing a good seedbed for *P. menziesii* regeneration. At higher elevations, *P. menziesii* does not occur in some stands, perhaps because such stands are more nearly climax; or disturbance by fire

may be less effective in initiating its regeneration at the colder limits of the habitat type. Alternatively, the somewhat colder environment at higher elevations may simply exceed the reproductive tolerance of *P. menziesii*.

In contrast, *Populus tremuloides* is an important tree throughout the ABLA/EREX HT. Dense *P. tremuloides* clones are often short-lived, and are replaced by conifers within a century. However, occasional tall trees can persist in the overstory canopy of conifer-dominated stands that are between 200 and 300 years old. *Populus tremuloides* sprouting may be stimulated by logging and burning practices that open the canopy and warm the soil (Jones and DeByle 1985, Schier et al. 1985).

***Abies lasiocarpa*/*Rubus parviflorus* habitat type (ABLA/RUPA; subalpine fir/western thimbleberry)**

We found the ALBA/RUPA HT (fig. 11) in the Mogollon Mountains, Gila National Forest, Glenwood and Wilderness Ranger Districts.

Vegetation.—*Abies lasiocarpa* is present, usually in all sizes, and always with 40 to 520 stems less than 4.5 feet tall per acre (99 to 1,285 per ha). *Picea engelmannii* usually is subordinate. In some stands, *Pseudotsuga menziesii* dominates, exhibiting abundant regeneration in successional *Populus tremuloides* stands; there is less regeneration in more mature stands.

Both tall and low shrub layers are present, with cover ranging from 15–55% in our plots. *Acer glabrum* and



Figure 10.—*Abies lasiocarpa*/*Erigeron eximius* habitat type, typical phase. This type, common between 9,400 and 10,200 feet (2,860 and 3,100 m) in the study area, provides opportunities for timber and wildlife management. A forb cover of 10% to 75% or more exceeds cover of the less prominent graminoids and shrubs.



Figure 11.—*Abies lasiocarpa*/*Rubus parviflorus* habitat type. White-water Canyon, Mogollon Mountains, 8,140 feet (2,481 m) elevation. A diverse and luxuriant undergrowth, with thermal protection provided by a dense overstory, make this habitat type a preferred wildlife summer habitat.

Rubus parviflorus always were present, each with coverage ranging from a trace to 20%. Other shrubs present in at least half our plots were *Holodiscus dumosus*, *Lonicera utahensis*, *Ribes pinetorum*, and *Robinia neomexicana*. *Vaccinium myrtillus* had less than 1% cover, and usually was absent.

Herbaceous cover varies from 1% to 35%, with many species present in trace amounts. We always found *Bromus ciliatus*, *Geranium richardsonii*, *Goodyera oblongifolia*, and *Ramischia secunda* in the plots. The following plants often were present: *Artemisia franserioides*, *Clematis pseudoalpina*, *Disporum trachycarpum*, *Epilobium angustifolium*, *Osmorhiza depauperata*, *Pteridium aquilinum*, *Senecio cardamine*, *Smilacina racemosa*, *Viola canadensis*, and *Zygadenus elegans*.

Physical setting.—The ABLA/RUPA HT occurs on moist, protected sites between 8,140 and 9,640 feet (2,481 and 2,938 m) elevation on northwest and northeast aspects. It is found at streamsides, in draws, and on middle and lower slopes with gradients that vary between 20% and 60%. Soils have not been studied in detail, but often appear as cobbly or very cobbly phases of Cryoboralfs and Cryoborolls at the warm extreme of the cryic soil temperature regime. They appear more productive than soils found in many other *Abies lasiocarpa* or *Picea engelmannii* habitat types.

Adjacent habitat types.—Adjoining colder or wetter sites may support forests of the ABLA/EREX HT or the ABLA/VAMY HT, RUPA phase. Less moist sites support ABCO/QUGA, ABCO/ACGL, or ABCO/Sparse HT's.

Discussion.—The ABLA/RUPA HT was first described by Moir and Ludwig (1979). It is closely related to the ABLA/VAMY HT, RUPA phase and the ABLA/EREX HT. The varied undergrowth composition, which provides browse and forage, and the diverse structure of the stand—composed of an herbaceous layer, two shrub layers, and various sizes of trees—make this type excellent habitat for numerous wildlife species.

***Picea pungens* Series**

***Picea pungens*/Senecio cardamine habitat type (PIPU/SECA; blue spruce/cardamine groundsel)**

We found the PIPU/SECA HT (fig. 12) in the White and Blue Mountains, Apache National Forest, along the East Fork of Thomas Creek and along Hannagan Creek.

Vegetation.—*Abies concolor* and *Pseudotsuga menziesii* were overstory dominants in our stands, with *Picea pungens* important, especially as regeneration. *Pinus strobiformis*, *Picea engelmannii*, *Abies lasiocarpa*, and *Populus tremuloides* were present in some plots, with only *Picea engelmannii* and *Populus tremuloides* occurring as mature trees.

A luxuriant ground cover of forbs, including *Senecio cardamine*, and the low cover of shrubs (less than 5%) helps to identify the PIPU/SECA HT. The low shrubs, *Pachistima myrsinites* and *Rubus parviflorus*, usually were present, and 11 other shrub species sometimes were found.



Figure 12.—*Picea pungens*/Senecio cardamine habitat type. This type, found on East Fork, Thomas Creek, and Hannagan Creek, Apache National Forest, 8,600 to 8,800 feet (2,620 to 2,680 m) elevation, has a luxuriant forb layer, with shrubs poorly represented. *Senecio cardamine* predominates in photograph; other species are *Carex foena*, *Fragaria americana*, and *Geranium richardsonii*.

Grass cover varied from 1% to 27% of the area, with *Bromus ciliatus* and *Carex foenea* dominant. Those two species plus *Carex rossii*, *Koeleria nitida*, and *Poa fendleriana* are characteristic species of the habitat type. *Festuca arizonica*, *F. sororia*, and *Muhlenbergia montana* were absent from our plots.

Forbs were dominant in the herbaceous layer. Depending on the sample plot, *Thermopsis pinetorum*, *Senecio cardamine*, or *Fragaria americana* exhibited the greatest coverage. Forb coverage ranged from 24% to 61%, with *Senecio cardamine* always present. Other species often found included: *Fragaria americana*, *F. ovalis*, *Geranium richardsonii*, *Lathyrus arizonicus*, *Pteridium aquilinum*, *Senecio wootonii*, *Viola canadensis*, *Pedicularis grayi*, and *Ramischia secunda*.

Physical setting.—Our plots were found from 8,640 to 8,800 feet (2,633 to 2,682 m) elevation on northerly aspects and steep slopes (between 48% and 54%). They were on upper, middle, and lower positions of the slope.

Adjacent habitat types.—The PIPU/SECA HT lies between mixed conifer and *Picea engelmannii*-*Abies lasiocarpa* habitat types, and adjoins types in the *Abies concolor*, *Abies lasiocarpa*, and *Picea engelmannii* series.

Discussion.—We have subdivided the *Picea pungens*-*Picea engelmannii*/Senecio cardamine habitat type of Moir and Ludwig (1979) into the PIPU/SECA and PIEN/SECA HT's, with some of their plots assigned to other types, based on our more intensive sampling in the Gila

and Apache National Forests, which comprise the center of distribution for *Senecio cardamine*. This habitat type is restricted to the areas described above. It has minor importance because of the small total area it covers, but may be locally important for visual quality, timber, livestock, and wildlife as noted in Moir and Ludwig (1979).

***Picea pungens*/Erigeron eximius habitat type
(PIPU/EREX; blue spruce/forest fleabane)**

Our plots were in the Mogollon and Mimbres Mountains, in the Gila and Cibola National Forests. They were found in the Glenwood, Mimbres, Reserve, Wilderness, and Magdalena Ranger Districts, but the type probably occurs throughout the study area on suitable sites.

Vegetation.—*Pseudotsuga menziesii* and *Picea pungens* are the major climax trees, both with abundant regeneration in mature stands. *Abies concolor* is a minor climax tree, when present, which usually regenerates less abundantly than *Picea pungens* or *Pseudotsuga menziesii*. Seral trees are *Pinus ponderosa*, *Pinus strobiformis*, and *Populus tremuloides*.

The undergrowth in the PIPU/EREX HT is characteristically herbaceous and dominated by forbs (fig. 13). In some stands, graminoids also are conspicuous, but shrubs usually are minor.

Shrub cover was less than 10% in most plots, but may be as high as 44%. The most dominant shrubs were *Quercus gambelii*, *Acer glabrum*, and *Lonicera arizonica*. Those which occurred most consistently on different plots were: *Quercus gambelii*, *Rosa* spp., and *Rubus parviflorus*.

Graminoid coverage ranged between 3% and 51%, but most plots contained from 10% to 25%. Graminoids that were dominant on different plots included *Bromus ciliatus* (the only grass found on all the plots), *Poa fendleriana*, *Festuca arizonica*, *Koeleria nitida*, *Muhlenbergia montana*, and *Carex foenea*. In addition, other sedges often were found on the plots.



Figure 13.—*Picea pungens*/Erigeron eximius habitat type. This forb-rich type is found from 7,600 to 9,050 feet (2,316 to 2,758 m) throughout the study area in canyon bottoms and on moist side slopes. It is important for wildlife and esthetics.

Forbs covered 18–97% of the area in the plots, but a 20–70% range included most of the plots. Forbs covered about 1.4 to 27 times more area than graminoids on any one plot. Sixteen species expressed dominance over a number of different plots, but *Achillea millefolium* occurred with the highest frequency. Characteristic species are *Artemisia franserioides*, *Fragaria* spp., *Erigeron eximius*, *Campanula rotundifolia*, *Cystopteris fragilis*, *Dugaldia hoopesii*, and *Pseudocymopterus montanus*. *Rudbeckia laciniata*, a forb found on wet sites, was absent from our plots, although *Prunella vulgaris* and *Actaea rubra*, also typical of wet sites, were sometimes found.

Physical setting.—Lower sites from 7,820 to 8,450 feet (2,383 to 2,575 m) tend to lack *Erigeron eximius* and are typified by *Fragaria* spp. and *Achillea millefolium*. Such plots were found on all aspects on lower slopes with subsurface water flow and on streamside locations one meter or more above the summer water level. In contrast, plots with *Erigeron eximius* were found between 8,040 and 9,050 feet (2,450 and 2,758 m) on sideslopes and benches on northerly aspects, except above 9,000 feet (2,743 m), where they were found on southeastern aspects. They apparently depended less on subsurface water, although most of those plots also were in lower slope or canyon bottom sites.

Adjacent habitat types.—Drier upslope sites may support the ABCO/QUGA, PSME/MUVI, and PSME/QUGA HT's. When the PIPU/EREX HT is on north slopes, stands representing ABCO/Sparse and ABLA/EREX HT's may be found upslope. On south slopes, the ABCO/MUVI, PIPO/MUVI, PIPO/QUGR, and PIPO/FEAR HT's were found adjacent to the PIPU/EREX HT. The PIPU/CAFO HT can be interspersed with the PIPU/EREX HT. In moister sites, the PIPU/POPR HT occurs. When the PIPU/EREX HT is on a slope with a northerly aspect, lower sites may support the ABLA/EREX HT. The PIPU/EREX HT often occurs as a stringer in canyon bottoms with drier, warmer types on either side. Types from different series often adjoin the PIPU/EREX HT at its upper and lower edges.

Discussion.—These herb-rich *Picea pungens* forests have a variable undergrowth composition, but always are characterized by forb dominance. Moir and Ludwig (1979) described a *Picea pungens*-*Picea engelmannii*/Erigeron superbus habitat type, which we have subdivided, separating the PIEN/EREX and PIPU/EREX HT's because of the overstory difference. We added to those plots representing the PIPU/EREX HT several herb-rich plots which lacked *Erigeron eximius*. DeVelice et al. (1986) also described the PIPU/EREX HT as we have. Alexander et al. (1984a) described a *Picea pungens*/*Fragaria ovalis* habitat type, named in conjunction with a preliminary classification, including a PIPU/FROV HT, presented in an earlier manuscript of this paper. Their PIPU/FROV HT may be equivalent to our PIPU/EREX HT, but there are some differences, notably in shrub coverage and species.

This habitat type, while restricted in area, is commercially and esthetically important. It is intrinsically resilient, but is subject to abuse because it is easily ac-

cessible to people and animals. Its occurrence in canyon bottom stands and its luxuriant herbaceous cover situated between less luxuriant types on steep hillsides create a travel lane for wild animals, livestock, and humans. Improper use of the type may adversely affect vegetation, soils, and groundwater levels. For example, overgrazing can cause a decrease in *Carex* spp., grasses, and *Erigeron eximius*, and an increase in *Achillea millefolium*, *Lathyrus arizonicus*, *Pseudocymopterus montanus*, *Prunella* spp., and *Dugaldia hoopesii*. Our plots showed intensive use by deer, elk, and squirrels.

Because of the better soil-plant moisture relationships associated with this type, timber growth is likely to be rapid, but we detected windthrow and signs of dwarf mistletoe (*Arceuthobium* spp.) infestations on *Pseudotsuga menziesii* and *Picea pungens*.

***Picea pungens*/Carex foenea habitat type (PIPU/CAFO; blue spruce/silvertop sedge)**

We found this type in the White Mountains and Blue Mountains of Arizona, on the Springerville and Alpine Ranger Districts of the Apache National Forest. It probably occurs elsewhere in the study area, as is evident from the widespread presence in other parts of Arizona and New Mexico (Moir and Ludwig 1979, Alexander et al. 1986, DeVelice et al. 1986).

Vegetation.—*Picea pungens* and *Pseudotsuga menziesii* usually are climax codominants, both with at least light or moderate regeneration (fig. 14). *Pinus ponderosa*,



Figure 14.—*Picea pungens*/Carex foenea habitat type. This habitat type is found on ridges and slopes between 7,840 and 9,400 feet (2,389 and 2,865 m) elevation. The strongly herbaceous undergrowth is dominated by sedges. It is a scenic type and is productive for timber and forage.

Pinus strobiformis, and *Populus tremuloides* are conspicuous seral trees. *Abies concolor* usually is absent. Colder sites may have small amounts of *Picea engelmannii*, with regeneration less abundant than that of *Picea pungens* and *Pseudotsuga menziesii* combined.

Shrubs usually were minor in this type. The normal range of cover was 0–4%, and no single species was consistently present. *Juniperus communis*, *Rubus parviflorus*, and *Rubus strigosus* were common.

The ground vegetation layer is strongly herbaceous, with graminoids providing the greatest visual impression, although their actual coverage may be less than that of forbs. Rhizomatous sedges may have greater coverage than bunchgrasses.

The graminoid component was diverse, and *Carex foenea* was the most characteristic species. Other graminoids frequently found were *Carex rossii*, *Festuca arizonica*, *Koeleria nitida*, and *Muhlenbergia virescens*. Notably absent was *Poa pratensis*. Graminoid cover ranged from 8% to 23%.

Forbs were unusually diverse and important components, having between 1% and 31% cover, but none were consistently present nor dominant. Some characteristic ones were *Campanula rotundifolia*, *Erigeron eximius*, *Fragaria ovalis*, *Haplopappus parryi*, *Pseudocymopterus montanus*, *Senecio neomexicanus*, *Senecio wootonii*, *Townsendia formosa*, and *Viola canadensis*.

Physical setting.—Sampled stands ranged from 7,840 to 9,400 feet (2,389 to 2,865 m) elevation, from ridges to lower slopes mostly paralleling drainages. Slope gradients varied from 0% to 50%, mostly on southwest aspects, except at lower elevations where the type was found on northerly aspects. Soils do not appear to be phreatic, at least within the upper horizons. Rather, it has been suggested that cold air drainage is important for most of the *Picea pungens* habitat types, including the PIPU/CAFO HT (Layser and Schubert 1979). The soil temperature regime is generally interpreted as being at the cold edge of the frigid zone.

Adjacent habitat types.—Grassy parklands may border this habitat type. Adjoining forests may include the ABLA/EREX, ABCO/ACGL, ABCO/FEAR, PIPO/FEAR, and PIPU/POPR HT's.

Discussion.—Moir and Ludwig (1979) described a PIPU/CAFO HT. We used their plots and ours to provide better resolution, reclassifying some of their PIPU/CAFO HT plots into a separate PIPU/FEAR HT. The PIPU/CAFO and PIPU/FEAR HT's described here would be equivalent to the *Pseudotsuga menziesii* phase, PIPU/CAFO HT, of Moir and Ludwig (1979). DeVelice et al. (1986) and Alexander et al. (1986) also described a PIPU/CAFO HT similar to ours.

Forb dominance in this habitat type may be natural in some stands, but graminoids have a significant amount of cover and impart a visual impression of dominance. Forb dominance also may be induced by grazing. The strong forb component shows the relationship of the PIPU/CAFO HT with the PIPU/EREX HT. In instances where forb dominance is slight and the graminoid component is strong, site factors may be important in distinguishing between these two habitat types.

Two *Picea pungens* stands were found with strong shrub components, but species composition in the sampled plots was such that we could not assign the stands to either the PIPU/COST HT (Alexander et al. 1986) or the PIPO/FROV HT (Alexander et al. 1984a). Instead, we classified those stands as a PIPU/CAFO HT and a PIPU/EREX HT based on herbaceous dominance.

The PIPO/CAFO HT is very productive for timber and forage and is esthetically attractive because of tree species diversity and association with meadows.

***Picea pungens*/Festuca arizonica habitat type
(PIPU/FEAR; blue spruce/Arizona fescue)**

We found the PIPU/FEAR HT in the Mogollon and White Mountains, Gila and Apache National Forests; specifically the Springerville, Alpine, Reserve, and Wilderness Ranger Districts.

Vegetation.—*Picea pungens* and *Pseudotsuga menziesii* are climax trees in this type (fig. 15). *Pinus ponderosa* is late seral, but often is codominant with the climax trees in stands that are several hundred years old. *Abies concolor* usually is absent, but when present, its regeneration is less than that of *Picea pungens*. *Populus tremuloides* is absent, or is found only locally in small, short-lived clones.



Figure 15.—*Picea pungens*/Festuca arizonica habitat type. Upper Negro Creek, Mogollon Mountains, 7,560 feet (2,304 m) elevation. This habitat type is dominated by *Picea pungens*, *Pseudotsuga menziesii*, and a luxuriant grass undergrowth; it occupies unique and unusual sites.

Shrubs are unimportant, although sometimes present. Shrub coverage in our plots was less than 5%.

Undergrowths are dominated by assorted bunchgrasses, but rhizomatous sedges often are present. Grass cover varies from 3% to 68%. *Festuca arizonica* or *Muhlenbergia virescens* usually dominate, but *Poa fendleriana* or *Bromus ciliatus* may be dominant on north slopes. The only grass found on all plots was *Koeleria nitida*. Other graminoids frequently found were *Carex foenea* and *Muhlenbergia montana*.

Forb coverage ranged from a trace to 62%, but most commonly from 6% to 35%. Many species were represented, but none were consistently found or consistently dominant. Typical forbs were *Achillea millefolium*, *Erigeron eximius*, *Fragaria ovalis*, *Haplopappus parryi*, *Penstemon barbatus*, *Senecio neomexicanus*, and *Senecio wootonii*.

Physical setting.—The PIPU/FEAR HT occurs between 7,560 and 9,120 feet (2,304 and 2,779 m) elevation on all aspects and slope steepnesses. Above 9,000 feet (2,743 m), it is found on southerly aspects and in all positions on the slope. Below 8,300 feet (2,530 m), it occurs on northerly aspects of lower slopes. Soil subgroups are highly varied and include Udic Argiborolls, Udic Haploborolls, Lithic Haploborolls, Eutric Glossoborolls, Typic Dystochrepts and Typic Haplustolls.

Adjacent habitat types.—Drier sites support PSME/MUVI and PIPO/FEAR HT's. When the PIPU/FEAR HT occurs at lower elevations on lower slopes, the PIPO/FEAR HT may exist upslope. Ecotones exist with these types on sideslopes, and they may contain some accidental *Picea pungens* because of the proximity of a consistent seed source. The ABCO/FEAR HT also may form ecotones with the PIPU/FEAR HT. Where more moisture is available, the PIPU/CAFO or PIPU/EREX HT's are adjacent to the PIPU/FEAR HT. The PIPU/POPR HT is found in drainage bottoms below slopes that support the PIPU/FEAR HT.

Discussion.—Intermediate stands between the PIPU/FEAR and PIPU/EREX HT's were found in our study, and plots in these situations with low total herbaceous cover were retained in the PIPU/FEAR HT, regardless of dominance by forbs. Because the PIPU/FEAR HT occurs on slopes, it is not as subject to overuse by livestock as are some other *Picea pungens* habitat types. It is productive, and provides good forage for cattle and elk, while abundant forbs make it desirable for deer and sheep. As tree stands mature, *Festuca arizonica* and *Muhlenbergia montana* decrease, but remain in openings. The PIPU/FEAR and PIPO/FEAR HT's merge gradually in ecotone areas which support a mixture of both types, especially on east exposures. These grassy blue spruce stands can be very scenic, having high esthetic and recreational values. Little bare ground occurs in the PIPU/FEAR HT under natural conditions. The combined moss plus litter cover in our plots varied from 75% to 95%. The soil probably absorbs precipitation readily, resulting in an erosion-resistant watershed.

The PIPU/FEAR HT also was described by DeVelice et al. (1986) in northern New Mexico.

***Picea pungens*/*Poa pratensis* habitat type
(PIPU/POPR; blue spruce/Kentucky bluegrass)**

This type, widespread throughout New Mexico (Moir and Ludwig 1979), was found at only one site in the present study (fig. 16). The sole location was on Little Turkey Creek in the Mogollon Mountains, in the Wilderness Ranger District, Gila National Forest.

Vegetation.—The basic characteristics of this type are the presence of *Picea pungens* and an extremely rich herbaceous layer in a streamside location. The general appearance of the association is grassy, with significant forb cover. *Poa pratensis* is always present. In our plot, *Picea pungens* was dominant, with *Pinus strobiformis* and *Pseudotsuga menziesii* present. Shrub, graminoid, and forb cover was 8%, 112%, and 46%, respectively. The importance of shrubs probably varies with the nature of the streamside; our plot included *Salix bebbiana*, *Rosa* spp., *Alnus* spp., and *Potentilla fruticosa*.

Physical setting.—The plot occurred at 8,000 feet (2,438 m) elevation, at the lower end of the range that extended up to 9,100 feet (2,774 m) in the study by Moir and Ludwig (1979). This type occurs only on alluvial soils adjacent to perennial streams.

Adjacent habitat types.—Adjacent types include PIPU/FEAR and PSME/MUVI HT's. Tree cover is often sparse in this type.



Figure 16.—*Picea pungens*/*Poa pratensis* habitat type. This habitat type is uncommon but widespread throughout the southwest between 8,000 and 9,100 feet (2,438 and 2,774 m) elevation. It is attractive for commercial and recreational activities. Undisturbed stands can rarely be found because of intensive use in the past.



Figure 17.—*Abies concolor*/*Erigeron eximius* habitat type. Apache Kid-Cowboy area of the San Mateo Mountains, 9,500 feet (2,895 m) elevation. A luxuriant undergrowth, including *Bromus ciliatus*, is found under the *Abies concolor* and *Pseudotsuga menziesii* overstory. Tree site quality is moderate to good.

Discussion.—This streamside *Picea pungens* habitat is closely related to the PIPU/COST HT (Alexander et al. 1986). Many palatable browse and herbaceous species occur in the PIPU/POPR HT. The type is susceptible to overuse by livestock because of the palatable plants and its topographic location on flat land adjacent to water. It also is a highly esthetic type, with other amenities such as fishing; it often is used for campgrounds. The type probably is naturally resilient, but use frequently exceeds its ability to recover from disturbance. Very few good examples of this type exist, and those remaining can be lost to soil erosion and lowered water tables unless protected.

***Abies concolor* Series**

***Abies concolor*/*Erigeron eximius* habitat type
(ABCO/EREX; white fir/forest fleabane)**

This habitat type was found in the Black Range, San Mateo, Mimbres, and Mogollon Mountains in the Gila and Cibola National Forests.

Vegetation.—*Abies concolor* and *Pseudotsuga menziesii* form a canopy over a luxuriant undergrowth of *Bromus ciliatus*, which is characteristic of this type (fig. 17). There is a dramatic decrease in *Abies concolor* between the 0–2 and 2–10 inch d.b.h. classes (0–5.1 and 5.1–25.4 cm); there are 130 to 8,400 stems per acre (321 to 20,756 per ha) in the smaller class and 10 to 230 per acre (25 to 568 per ha) in the larger size class, respectively. *Pinus strobiformis* is prominent in late seral stands. *Pinus ponderosa* is occasionally present, sometimes with moderate regeneration which does not survive competition with *Abies concolor* and *Pseudotsuga menziesii*. *Abies lasiocarpa* is absent or accidental, and *Picea engelmannii*, if present, is represented by less than 25 stems per acre in the 2- to 10-inch (5.1–25.4-cm) size class.

Although coverage of shrubs (mostly *Acer glabrum*) may be 0% to 60%, it is less than that of grasses or forbs. Grasses, dominated by *Bromus ciliatus*, cover 6% to 95%.

Forbs cover 8% to 124%, including such species as *Achillea millefolium*, *Artemisia franserioides*, *Erigeron eximius*, *Fragaria ovalis*, *Haplopappus parryi*, *Lathyrus arizonicus*, *Pteridium aquilinum*, *Pyrola chlorantha*, *Senecio bigelovii*, *Smilacina stellata*, and *Viola canadensis*. Plants notable by their absence include *Berberis repens*, *Juniperus communis*, *Vaccinium myrtillus*, and *Festuca arizonica*. On some sites, total grass cover exceeds 80% and is dominant over forbs. *Trisetum montanum* and *Festuca sororia* have more than 1% coverage. On other sites, *Festuca sororia* and *Trisetum montanum* are absent, with grass cover less than 40%. Forbs approach or exceed grass coverage. Within this latter group, our plots in the Mimbres Mountains differ from the typical expression of the type by having only 17% to 34% herbaceous coverage, with *Erigeron eximius* absent and *Bromus ciliatus* and *Agropyron arizonicum* sharing dominance.

Physical setting.—Most plots were on deep soils and gentle slopes. Light ground fires occurred with a 30-year frequency. *Festuca sororia* was present on upper slopes (3%–50% gradients), ridgetops, and northerly aspects from 9,560 to 9,640 feet (2,913 to 2,938 m) elevation. When *Festuca sororia* was absent, plots were in gentle mesic draws and ravines and on slopes varying from 10% to 25% with northerly aspects (one exception). Elevations of plots ranged from 8,720 to 9,600 feet (2,657 to 2,926 m).

Adjacent habitat types.—Moister sites on warmer, shallow soil support the ABCO/QUGA HT. Drier sites support the PSME/BRCI HT and the *Muhlenbergia virescens* phase of the ABCO/QUGA HT. Higher elevations support ABCO/MUVI stands.

Discussion.—Moir and Ludwig (1979) originally described this type as the *Abies concolor*-*Pseudotsuga menziesii*/*Erigeron superbus* habitat type. We shortened the name and used *Erigeron eximius* to conform with presently accepted taxonomy (appendix B).

Populus tremuloides and *Robinia neomexicana* dominate seral stands. Care may be required during logging and prescribed burning to prevent excessive increases in shrub density. *Pseudotsuga menziesii* was heavily infested with dwarf mistletoe (*Arceuthobium* spp.), and some insect defoliation was noticed in our plots. Site quality for trees is moderate to good for both *Pseudotsuga menziesii* and *Abies concolor*.

***Abies concolor*/Sparse habitat type (ABCO/Sparse; white fir/sparse)**

The ABCO/Sparse HT is very common throughout the study area and elsewhere (Moir and Ludwig 1979) (fig. 18).

Vegetation.—This type is characterized by *Abies concolor* and *Pseudotsuga menziesii* dominance; however, *Abies concolor* may be absent in the overstory. A prominent shrub layer of *Robinia neomexicana*, *Quercus gambelii*, *Symphoricarpos oreophilus*, *Sambucus* spp., and *Lonicera* spp. is present, but none are constant. The herbaceous layer may be composed of numerous species,



Figure 18.—*Abies concolor*/Sparse habitat type. Crest Trail, Mimbres Mountains, 9,160 feet (2,791 m) elevation. This habitat type has an obvious tall shrub layer, with mosses and lichens dominating herbs.

but it usually provides less than 2% total ground cover (occasionally as much as 10%). Mosses and lichens may be important on microsites free of tree litter. The following shrubs were not found in our plots: *Acer grandidentatum*, *Cornus stolonifera*, *Jamesia americana*, and *Juniperus communis*. Openings in the ABCO/Sparse HT may have either a depauperate herbaceous layer with increased grasses, or a somewhat greater cover of forbs dominated by such species as *Pteridium aquilinum*, *Senecio wootoni*, *Hieracium fendleri*, and *Senecio neomexicanus*.

Physical setting.—Our plots were found from ridges to midslope (4–65% gradient) on all aspects between 8,550 and 9,480 feet (2,606 and 2,889 m) elevation.

Adjacent habitat types.—Moist drainage bottoms adjacent to stands of the ABCO/Sparse HT support *Abies concolor*, with extensive *Berberis repens* in the undergrowth. Some of these stands are in the ABCO/ACGL HT, and may lack *Berberis repens*. Drier sites support the ABCO/MUVI HT and both phases of the ABCO/QUGA HT. Dry ridges support the PSME/MUVI HT, with increased *Holodiscus dumosus* and *Robinia neomexicana* on rocky areas. Mossy patches may occur on shallow soils. The ABCO/Sparse HT can grade into grassy types in younger stands on drier sites.

Discussion.—The ABCO/Sparse HT was first described as the ABCO-PSME HT (sparse understory) by Moir and Ludwig (1979). Subsequently, the present name was applied by Alexander et al. (1984a) and DeVelice et al. (1986). The ABCO/Sparse HT resembles the ABCO/BERE and ABCO/SYOR HT's. (Youngblood and Mauk 1985), but there are some important differences.

Stands of *Abies concolor*, varying from 80 to 100 years old, that were reestablished following fire in the ABCO/Sparse HT, exhibited an undergrowth similar to the climax. Such stands also were characterized by fallen pole-sized stems of *Populus tremuloides*, which exhibited advanced root rot in 30-year old stands. An older *Populus tremuloides* clone in this type contained a similar undergrowth, with increased *Berberis repens*, *Bromus* spp., *Smilacina* spp., *Pterospora andromeda*, *Corallorhiza* spp.,

Fragaria ovalis, *Symphoricarpos oreophilus*, and *Robinia neomexicana*. Infection by dwarf mistletoe (*Arceuthobium* spp.) was less on *Pseudotsuga menziesii* than on other species in this type. Some windthrow was evident. In the Mogollon Mountains, between 8,700 and 9,200 feet (2,652 and 2,804 m) on upper northerly slopes, the PIEN/VAMY HT was found in draws below the ABCO/Sparse HT. In this situation, *Picea engelmannii* and *Abies lasiocarpa* reproduction was found in ABCO/Sparse stands, but such reproduction may not survive to become a component of the overstory. Similar areas may be devoid of these species because of a lack of seed source.

***Abies concolor*/Holodiscus dumosus (Scree) habitat type (ABCO/HODU (Scree); white fir/bush rockspirea (scree))**

We found the ABCO/HODU (Scree) HT in the Magdalena and San Mateo Mountains of the Cibola National Forest, New Mexico.

Vegetation.—Mature *Pinus strobiformis* and *Abies concolor* are less abundant than *Pseudotsuga menziesii*, but sometimes codominant with it. *Picea pungens*, *Picea engelmannii*, *Abies lasiocarpa*, *Juniperus* spp., and riparian trees are absent. Shrubs and graminoids are approximately equal in coverage (each with 1–25%), with trace amounts of numerous forb species. *Jamesia americana*, *Bromus ciliatus*, *Koeleria nitida*, *Allium cernuum*, and *Primula ellisiae* were always present in our plots. Other species included *Holodiscus dumosus* and *Festuca arizonica*.

Physical setting.—Our plots were located on mid-slopes with 50–60% gradients and northwest aspects, between 9,200 and 9,240 feet (2,804 and 2,816 m) elevation. The sites were typical of loose rock (scree) slopes (fig. 19), in that soil-water storage capacity and subsequent moisture availability for plants was low, except for deep-rooted species. Our plot data showed 13% to 30% exposed rock and 2% to 4% exposed soil as a thin layer over cobble scree.

Adjacent habitat types.—Almost any of the other mixed conifer types expected at this elevation could be found adjacent to the ABCO/HODU (Scree) HT, depending on nearby site conditions.

Discussion.—The ABCO/HODU (Scree) HT was described in northern New Mexico by DeVilce et al. (1986).

Canopy cover in this habitat type is low and timber production is poor. Dwarf mistletoe (*Arceuthobium* spp.) infestation is heavy on *Pseudotsuga menziesii* and *Pinus strobiformis*. Evidence of ground disturbance following use in this type is slight. This type is similar to other forest scree habitat types in enhancing groundwater recharge and providing special wildlife microhabitats.

***Abies concolor*/Acer glabrum habitat type (ABCO/ACGL; white fir/Rocky Mountain maple)**

The ABCO/ACGL HT is widespread throughout Arizona and New Mexico (Moir and Ludwig 1979), including the present study area (fig. 20). It was found in



Figure 19.—*Abies concolor*/Holodiscus dumosus (Scree) habitat type. Upper San Mateo Canyon, San Mateo Mountains, 9,360 feet (2,852 m) elevation. As in all high elevation scree sites, deep-rooted shrubs dominate the undergrowth, and groundwater recharge is an important function of the type.



Figure 20.—*Abies concolor*/Acer glabrum habitat type. Windy Point, Mogollon Mountains, 8,640 feet (2,633 m) elevation. This habitat type, with its obvious tall shrub layer, is common at moderately high elevations throughout the Southwest.

all three National Forests in the White, Mogollon, San Mateo, and Tularosa Mountains, wherever elevation was sufficient.

Vegetation.—*Abies concolor* and *Pseudotsuga menziesii* are dominant, with *Pinus strobiformis* occasionally codominant. *Picea pungens*, *Picea engelmannii*, and *Abies lasiocarpa* are present only in small sizes or in transitional areas. Mature *Pinus ponderosa* usually is absent, but it may dominate when originated by fire; more typically it persists as scattered individuals. *Abies con-*

color and *Pseudotsuga menziesii* seedlings are very abundant; 2 inch (5 cm) and larger stems much less so. Shrub cover, including *Acer glabrum*, exceeds that of herbaceous plants except in a few plots transitional to *Picea pungens* stands. Grasses and forbs each cover less than 40% of the ground. *Acer grandidentatum*, *Cornus stolonifera*, *Juniperus communis*, *Festuca arizonica*, *Muhlenbergia montana*, *Poa pratensis*, *Festuca sororia*, *Dugaldia hoopesii*, *Ligusticum porteri*, *Mertensia franciscana*, *Pteridium aquilinum*, and *Swertia radiata* are notably absent. Moir and Ludwig (1979) described this type as the ABCO-PSME/ACGL HT, which included plots that contained *Acer grandidentatum*. We separated those plots into a different type (ABCO/ACGR HT), and shortened the name of the original type to the ABCO/ACGL HT. Moir and Ludwig (1979) also classified one plot in the White Mountains as the *Berberis repens* phase of their ABCO-PSME/ACGL HT, but we found no other representative of that phase. *Jamesia americana* occurs on cobbly substrates, while *Muhlenbergia virescens* and *Pteridium aquilinum* dominate openings, which also contain more *Bromus* spp., *Symphoricarpos oreophilus*, and *Holodiscus dumosus*.

Physical setting.—Our plots occurred from streamside settings to upper slopes which generally faced north and exhibited gradients varying from 18% to 67%. Southerly slopes supported this type only at higher elevations or streamside settings. Typical elevations were between 8,100 and 9,800 feet (2,468 and 2,987 m).

Adjacent habitat types.—Moister sites support stands characterized by the ABLA/RUPA HT. Drier south-facing slopes support PSME/HODU (Scree) and ABCO/QUGA HT's. Adjacent higher elevations support PSME/QUGA, ABLA/RUPA, and ABCO/QUGA HT's. Lower slopes support *Picea pungens*-*Pseudotsuga menziesii* stands.

Discussion.—In addition to Moir and Ludwig (1979), this type was identified by Alexander et al. (1984a, 1986), Youngblood and Mauk (1985) and DeVelice et al. (1986). Although these descriptions represent the same habitat type, there may be a geographic gradient in plant species that warrants different phase designations in some areas.

Some spruce budworm activity was noted on *Pseudotsuga menziesii*. Game trails and browsing illustrated the high value of this type for big game. The presence of a tall shrub layer increases vertical diversity for birds, and a greater number of bird species might be expected here than in less diverse types.

***Abies concolor*/Muhlenbergia virescens habitat type (ABCO/MUVI; white fir/screwleaf muhly)**

Our plots were in the White and Mogollon Mountains and the Black Range in the Apache and Gila National Forests.

Vegetation.—*Pseudotsuga menziesii* and *Abies concolor* dominate, although *Abies concolor* sometimes is poorly represented in the overstory (fig. 21). Old individuals of *Pinus ponderosa* are present, usually with sparse reproduction. Although minor or absent in the overstory,



Figure 21.—*Abies concolor*/Muhlenbergia virescens habitat type. This type—found in the White and Mogollon Mountains and the Black Range—is dominated by *Pseudotsuga menziesii* and *Abies concolor*, with both forbs and grasses important in the undergrowth. It is found on ridges and side slopes from 8,000 to 9,700 feet (2,438 to 2,804 m) elevation.

Pinus strobiformis is present in the understory. *Picea pungens* may be accidental in small size classes. *Picea engelmannii*, *Abies lasiocarpa*, *Juniperus* spp., and riparian trees are absent. Shrubs have less than 5% coverage, and except for *Quercus gambelii* are minor components of the stand. *Muhlenbergia virescens* (more than 1% coverage) dominates grasses, with *Poa fendleriana* also present. In heavily shaded microsites, *Bromus ciliatus* may dominate. Grasses are important in the herbaceous layer, but forbs also are prominent. Occasionally, a single forb species such as *Lathyrus arizonicus*, *Pteridium aquilinum*, or *Senecio wootoni* may dominate the site. The following important indicators are absent from this type: *Acer glabrum*, *Acer grandidentatum*, *Berberis repens*, *Holodiscus dumosus*, *Jamesia americana*, *Quercus rugosa*, *Festuca arizonica*, *Trisetum montanum*, *Festuca sororia*, *Erigeron eximius*, *Ligusticum porteri*, *Mertensia franciscana*, *Senecio cardamine*, *Swertia radiata*, and *Valeriana capitata*. Where the overstory creates heavy shade, *Muhlenbergia virescens* may be reduced to presence value only. Some openings have increased amounts of *Muhlenbergia virescens*, but in openings where grass densities are reduced, patches of *Lupinus* spp. occur.

Physical setting.—The ABCO/MUVI HT typically is found on ridges down to midslopes, with 9–55% gradients and southerly aspects; but it may occur on all aspects. The typical elevational range is 8,000–9,200 feet (2,438–2,804 m).

Adjacent habitat types.—Moister sites support herb-rich *Picea pungens*-*Pseudotsuga menziesii* stands. Dry upper slopes support the PIPO/MUVI HT, with abundant *Pteridium aquilinum*. Higher elevations support phases of the ABCO/QUGA HT, while lower slopes support the PSME/MUVI HT and habitat types associated with *Picea pungens*-*Picea engelmannii* stands.

Discussion.—*Populus tremuloides* may be restricted to deeper, finer-textured soils in some stands of this type. In other stands, patches of *Quercus gambelii* were present, but *Populus tremuloides* was not. Spruce budworm

defoliation was noted on *Abies concolor* and *Pseudotsuga menziesii* regeneration in some stands. This type has been extensively logged and grazed in some areas. Plants that increase after logging are *Muhlenbergia virescens*, *Pteridium aquilinum*, and *Robinia neomexicana*.

***Abies concolor*/Quercus gambelii habitat type (ABCO/QUGA; white fir/Gambel oak)**

The ABCO/QUGA HT is widely distributed throughout the study area (fig. 22), and also is found throughout Arizona and New Mexico (Moir and Ludwig 1979).

Vegetation.—Both *Abies concolor* and *Pseudotsuga menziesii* are climax dominants, with *Pinus strobiformis* a major late seral component; all are represented in the reproduction size-class. *Pinus ponderosa* often dominated stands in our plots, and occasionally *Pinus strobiformis* was dominant. *Pinus ponderosa* reproduction may sometimes reach 120 stems per acre (296 per ha), but does not persist as older age classes in mature stands. The undergrowth is dominated by *Quercus gambelii*, or at least *Quercus gambelii* is well represented, with more than 5% cover in a tall shrub or small tree layer. *Robinia neomexicana* is more dense on cobble-scrub and rocky areas. *Festuca arizonica*, *F. sororia*, and *Trisetum montanum* are absent. The typical (*Quercus gambelii*) phase has less than 4% *Muhlenbergia virescens* coverage, whereas the *M. virescens* phase has considerably more. The *Muhlenbergia virescens* phase of this



Figure 22.—*Abies concolor*/*Quercus gambelii* habitat type, typical phase. Apache Kid Trail, San Mateo Mountains, 8,200 feet (2,499 m) elevation. Site quality for timber often is poor in this habitat type, with potential brush and grass competition hindering tree regeneration following disturbance.

habitat type is distinguished from the ABCO/MUVI HT by a 5% or more cover of *Quercus gambelii*.

Physical setting.—Our plots were mostly on ridges and side slopes, but some occurred on lower slopes at lower elevations. Elevations varied from 7,400 to 9,560 feet (2,255 to 2,913 m) and slope gradients from 40% to 77%. This type occurs on steep slopes, with soils varying from thin and rocky to deep and loamy. Aspects supporting the *Quercus gambelii* phase were northern or southeastern, except that at higher elevations some stands occurred on southwestern exposures. The *Muhlenbergia virescens* phase was found more on southern aspects, except at lower elevations. However, on shallow soils, plots were found on northern slopes throughout the elevational range of the phase.

Adjacent habitat types.—Ecotones with ABCO/QUGA and PSME/QUHY HT's are typical. Moister sites supported the ABCO/Sparse and ABCO/ACGL HT's. Drier sites supported PSME/MUVI and PIPO/MUVI HT's. Lower canyon-bottom sites supported the PIPU/FROV HT. Rocky ridges with skeletal soils and other dry edaphic sites supported the PSME/QUHY HT, while steep west-facing upper slopes supported ABCO/Sparse stands.

At elevations where the ABCO/QUGA HT occurs on north-facing slopes, several habitat types may be encountered with changes in aspect. For example, beginning on steep southerly slopes and proceeding in a northerly direction around the slope, vegetation progresses from chaparral through pinyon-juniper to the PSME/QUGA HT (with *Pinus ponderosa* dominant in seral stands), continuing into the PSME/MUVI HT (with sparse forbs), and finally into the ABCO/QUGA HT.

Discussion.—The ABCO/QUGA HT was identified by Moir and Ludwig (1979), Alexander et al. (1984a, 1986), Youngblood and Mauk (1985), and DeVelice, et al. (1986).

Succession following fire or other disturbance usually results in increased densities of *Quercus gambelii*, *Robinia neomexicana*, *Lonicera* spp., and possibly *Muhlenbergia virescens*. Herbaceous cover may be reduced to 5% as the canopy closes. Timber site quality in the *Quercus gambelii* phase often was poor, with short and round-topped trees. Band-tailed pigeons (*Columba fasciata*) were nesting in this type.

***Abies concolor*/Robinia neomexicana habitat type (ABCO/RONE; white fir/New Mexico locust)**

The ABCO/RONE HT was described by Moir and Ludwig (1979) from two somewhat disturbed stands in the Apache National Forest, Arizona. We located no additional sites.

Vegetation.—*Abies concolor* and *Pseudotsuga menziesii* are characteristic trees, with poor *Pseudotsuga menziesii* regeneration and abundant *Abies concolor* regeneration (about 300 stems per acre or 741 per ha). The high coverage of *Robinia neomexicana* is characteristic of the type (fig. 23). Also present in the plots were *Picea engelmannii*, *Pinus strobiformis*, *Populus tremuloides*, and *Pinus ponderosa*. Shrubs dominate the undergrowth with

45–75% cover. Forbs are subordinate to codominant with grasses in the herbaceous layer.

Physical setting.—This type occurs on volcanic ash or cinder soils, on gentle slopes at about 8,700 feet (2,652 m).

Adjacent habitat types.—This type was found on small knolls adjacent to other mixed conifer types such as the ABCO/QUGA HT.

Discussion.—The ABCO/RONE HT may be a fire-derived or logging-stimulated seral community. However, certain soil characteristics also may determine a strong dominance of *Robinia neomexicana*. Caution should be exercised in this habitat type because fire or logging activities will increase coverage of *Robinia neomexicana*, which will probably decrease tree regeneration.

***Abies concolor*/*Festuca arizonica* habitat type (ABCO/FEAR; white fir/Arizona fescue)**

This type was found in the White and Mogollon Mountains, Apache and Gila National Forests and the Magdalena Mountains, Cibola National Forest (fig. 24).

Vegetation.—*Abies concolor* and *Pseudotsuga menziesii* are codominant, with regeneration varying from more than 100 stems per acre (266 per ha) for *Abies concolor* and *Pseudotsuga menziesii* combined; to as much as 1,340 stems (3,330 per ha) for *Abies concolor* alone. *Pinus ponderosa* is codominant in late seral stands. *Picea pungens*, *Picea engelmanni*, and *Abies lasiocarpa* are absent or accidental.



Figure 23.—*Abies concolor*/*Robinia neomexicana* habitat type. Thickets of *Robinia neomexicana* and young *Pinus ponderosa* characterize openings on this site underlain by volcanic ash.



Figure 24.—*Abies concolor*/*Festuca arizonica* habitat type, typical phase. South Baldy Trail, Magdalena Mountains, 9,300 feet (2,834 m) elevation. A mixed conifer overstory and grass-dominated undergrowth make this habitat type important for cattle grazing and wild turkey nesting.

Based on coverage, shrubs and forbs were subordinate to codominant with grasses. In the *Festuca arizonica* phase, *Festuca arizonica* was the dominant herbaceous plant, with *Carex foenea*, *Bromus ciliatus*, *Muhlenbergia montana*, and *Sitanion hystrix* also present. *Berberis repens* was dominant under conifers on stony soils, but *Festuca arizonica* and *Muhlenbergia montana* dominated openings.

In the *Poa fendleriana* phase, the herbaceous layer was dominated by *Poa fendleriana*. *Robinia neomexicana* and *Bromus ciliatus* often were present, and *Festuca arizonica* was notably absent. This phase was earlier described by Moir and Ludwig (1979) as the ABCO-PSME/POFE HT.

Physical setting.—Moir and Ludwig (1979) found the type on ridges and gentle slopes or on moderate to steep east-, south-, or west-facing canyon slopes. They described the elevational range as 7,000 to 9,400 feet (2,134 to 2,865 m). Our plots in the *Festuca arizonica* phase were at 8,850 to 9,480 feet (2,697 to 2,889 m). The *Poa fendleriana* phase was found from 8,300 to 8,850 feet (2,529 to 2,697 m).

Adjacent habitat types.—Lower slopes may support habitat types having *Senecio cardamine* as the undergrowth indicator. Adjacent types included PIPU/CAFO, PIPU/FEAR, PIPU/EREX, and PSME/MUVI HT's.

Discussion.—Reasons for the absence of *Festuca arizonica* in the *Poa fendleriana* phase are unknown. It may be natural, or could be the result of overgrazing during early settlement. We did not feel justified in describing a distinct habitat type from the three plots in the *Poa fendleriana* phase.

We found abundant elk sign in the typical phase, perhaps because of greater graminoid cover and the preference of the animals for such forage. The type also is well adapted for grazing by livestock. It may be important as a brood area for wild turkeys (*Meleagris gallopavo*), because of the inherent capability of the tall grass to produce insects for young poults. In the *Poa fendleriana* phase, dwarf mistletoe (*Arceuthobium* spp.) was heavy on some tree species. Some windthrow was observed, and in one stand many trees were broken at the base.

***Abies concolor*/*Acer grandidentatum* habitat type (ABCO/ACGR; white fir/bigtooth maple)**

We had only one plot in this type, which varied somewhat from the ABCO/ACGR HT of cool canyon bottoms described by Moir and Ludwig (1979). Alexander et al. (1984a) described the type in the Lincoln National Forest. Suitable sites for this type are infrequent, but the type probably occurs throughout the study area where such sites exist (fig. 25).

Vegetation.—In our plot, *Pseudotsuga menziesii* was better represented than in the Arizona plots sampled by Moir and Ludwig (1979). *Abies concolor* dominated the stand, with *Pseudotsuga menziesii* and large *Acer negundo* important components. *Picea engelmannii* and *Abies lasiocarpa* were absent. *Acer grandidentatum* with diameters greater than 2 inches (5.1 cm) numbered 280



Figure 25.—*Abies concolor*/*Acer grandidentatum* habitat type. Upper Little Dry Creek, Mogollon Mountains, 7,360 feet (2,243 m) elevation. This infrequently occurring riparian habitat type has an extremely high value as a fish and wildlife habitat; it also serves as a fire barrier.

per acre (692 per ha). *Symphoricarpos oreophilus* also was present. Grasses dominated forbs. *Poa fendleriana*, *Bromus ciliatus*, *Fragaria americana*, and *Viola canadensis* were present.

Physical setting.—Our plot was typical of the site described by Moir and Ludwig (1979). It was on a subirrigated cobble alluvium, 6.5 feet (2 m) above the bed of an intermittent stream in a steep-sided, shady canyon, oriented southwest. The gradient of the plot was 7%. The elevation was 7,360 feet (2,243 m).

Adjacent habitat types.—This type usually is adjacent to the ABCO/QUGA HT. It is related to the ABCO/ACGL HT, and may adjoin it on some sites. Steep topography may result in the PSME/QUGA or even the PIPO/QUGA HT's occurring adjacent to the ABCO/ACGR HT.

Discussion.—We found abundant reproduction of young conifers in mature stands in this type, but subsequent survival was low. The importance of this riparian type for wildlife and fish habitat and as a fire barrier probably is much greater than its importance as a timber and grazing resource, particularly considering the small areas involved. The following excerpts from Moir and Ludwig (1979) describe the influence of logging in the ABCO/ACGR HT. "Logging probably accelerates growth and development of *Acer grandidentatum* as a result of increased light in the understory." Furthermore, "...strong dominance of the species in logged areas does not appear to retard conifer establishment."

***Abies concolor*/*Juglans major* habitat type (ABCO/JUMA; white fir/Arizona walnut)**

We found this type by Mineral Creek, Mogollon Mountains, in the Glenwood Ranger District, Gila National Forest (fig. 26). The habitat type probably occurs on suitable sites on western slopes of the Mogollon Mountains and perhaps in other ranges as well. Alexander et al. (1984a) described the ABCO/JUMA HT in the Lincoln National Forest.

Vegetation.—Large *Acer negundo*, *Juglans major*, and *Quercus gambelii* trees dominate the stand, with *Abies concolor*, *Pinus ponderosa*, and *Pseudotsuga menziesii* scattered. *Abies concolor* saplings may be abundant. The undergrowth probably is variable, but plants typical of moist but not wet sites, such as *Fraxinus* spp., *Ptelia* spp., *Toxicodendron rydbergii*, and *Vitis* spp., were present in our plot. The herbaceous layer included *Bromus ciliatus*, *Monarda menthaefolia*, *Pseudostellaria jamesiana*, and *Viola canadensis*.

Physical setting.—The single plot in this type was at 6,440 feet (1,962 m) elevation, with a southeast aspect. It was on a steep slope, 16 to 23 feet (4.8 to 7.0 m) above a permanent stream, but in a canyon-bottom environment. Soils were a cobbly-bouldery canyon detritus. Tree roots probably obtained yearlong moisture from the water table, but herbaceous plants likely were subjected to early summer drought. The site is occasionally flooded, but is above the normal flood level and the physical impact of flooding is limited.

Adjacent habitat types.—This type occurred above the adjacent riparian *Populus angustifolia* series, with chaparral and pinyon-juniper vegetation in higher positions on canyon sides.

Discussion.—While this type was represented by only one plot, it was sufficiently distinct to be classified as a separate riparian type, which was supported by another study (Alexander et al. 1984a).

Coniferous stocking was low, although young regeneration was abundant. Consequently, logging may pose problems because of the difficulty of regenerating the stand. Grasses are important to turkey and quail communities because they supply food and cover, and provide a substrate for insects, which are necessary for survival of young birds. Spring grazing may be detrimental to wildlife populations because of its effect on cover and insect populations when the young are vulnerable. Grasses also provide cover for rodents, which are an important unit in the predatory food chain. Deciduous trees in riparian areas are important to game and nongame animals because they moderate the microclimate and provide suitable conditions for a more luxuriant plant community than that found on adjacent sites.

***Pseudotsuga menziesii* Series**

***Pseudotsuga menziesii*/Arctostaphylos uva-ursi habitat type**
(PSME/ARUV; Douglas-fir/bearberry)

We found this type only in the San Mateo Mountains, Cibola National Forest (fig. 27).



Figure 26.—*Abies concolor*/*Juglans major* habitat type. Lower Mineral Creek, Mogollon Mountains, 6,440 feet (1,962 m) elevation. This habitat type is dominated by riparian hardwoods, with the undergrowth typical of upland sites.



Figure 27.—*Pseudotsuga menziesii*/Arctostaphylos uva-ursi habitat type. San Mateo Canyon, San Mateo Mountains, 8,800 feet (2,644 m) elevation. An extensive undergrowth of *Arctostaphylos uva-ursi* and low timber production potential characterize this type.

Vegetation.—Both *Pseudotsuga menziesii* and *Pinus strobiformis* are important, and *Arctostaphylos uva-ursi* has extensive coverage (more than 30% in our plots). Other shrubs, including species with tall form, were less important. *Bromus ciliatus* also was present.

Physical setting.—Our plots were on ridgetops between 9,800 and 9,900 feet (2,987 and 3,017 m).

Adjacent habitat types.—Warm, dry, lower slopes adjacent to the PSME/ARUV HT support the ABCO/FEAR HT, POFE phase and related habitat types.

Discussion.—Our plots lacked *Abies concolor*, but we observed a stand that contained *Abies concolor*, dense *Arctostaphylos uva-ursi*, *Bromus ciliatus*, *Achillea millefolium*, *Erigeron eximius*, and *Geranium richardsonii*, and was located on deep alluvium adjoining an intermittent creek at 8,800 feet (2,682 m) elevation. DeVelice et al. (1986) described a *Pinus flexilis*/*Arctostaphylos uva-ursi* habitat type, with less undergrowth coverage than in our plots; but otherwise similar to them. The occurrence of *Arctostaphylos uva-ursi* in the undergrowth of these various habitat types suggests some relationship in about their classification. Consequently, additional sampling is needed to clarify their status.

Fires have been extensive and severe in this type, resulting in *Populus tremuloides* becoming established as a major seral tree. Timber site quality apparently is low; trees are about 30 feet (9.1 m) tall with rounded or dead tops.

***Pseudotsuga menziesii*/*Holodiscus dumosus* (Scree) habitat type**
(PSME/HODU (Scree); Douglas-fir/bush rockspirea (scree))

We sampled this type only on Black Mountain in the Mogollon Mountains, Glenwood Ranger District, Gila National Forest (fig. 28). The habitat type probably is found on high elevation scree slopes in other mountain ranges as well.

Vegetation.—*Pseudotsuga menziesii* is dominant. *Pinus strobiformis* and *Populus tremuloides* also may be present. Shrubs dominate herbaceous plants, with 17–23% coverage. Forbs have 6% or less coverage, and dominate grasses, which have 1% or less. Typical plants are *Holodiscus dumosus*, *Salix scouleriana*, *Symphoricarpos oreophilus*, *Bromus ciliatus*, *Clematis pseudoalpina*, *Haplopappus parryi*, and *Smilacina stellata*.

Physical setting.—Our plot, on loose rock, was on a steep (57%) southerly slope at 9,600 feet (2,926 m) elevation. The site exhibited 80% exposed rock. The type appears to be limited to areas with loose surface rock, making water available only to deep-rooted species. Some plants may obtain water from pockets of soil perched on the unstable rocks. There was no exposed soil in our plot.

Adjacent habitat types.—Adjoining stands include various mixed conifer, *Picea engelmannii*, and *Abies lasiocarpa* habitat types, the nature of which depends on site factors that may vary considerably from the scree slopes on which the PSME/HODU (Scree) HT is found.

Discussion.—*Abies lasiocarpa* and *Picea engelmannii* may be present in this type, providing a seed source exists nearby (DeVelice et al. 1986). Ground disturbance would have little effect on aesthetics, the ecology of the site, or on germination and early establishment of tree seedlings. The sites would be difficult to log. They are important for groundwater recharge as with the ABLA/HODU (Scree) HT. Certain rodents such as Mexican woodrats (*Neotoma mexicana*), white-throated woodrats (*N. albigula*), and golden-mantled ground squir-



Figure 28.—*Pseudotsuga menziesii*/*Holodiscus dumosus* (Scree) habitat type. Black Mountain, Mogollon Mountains, 9,600 feet (2,926 m) elevation. Water is available only to deep-rooted species (shrubs and trees), except where it accumulates in soil pockets perched on unstable rock.



Figure 29.—*Pseudotsuga menziesii*/*Festuca arizonica* habitat type. Magdalena Mountains, 9,600 feet (2,926 m) elevation. This high elevation grassy type is dominated by *Festuca arizonica*.

rels (*Citellus lateralis*), and reptiles including the short-horned lizard (*Phrynosoma douglassii*) and rock rattlesnake (*Crotalus lepidus*) find excellent habitat in this type. The PSME/HODU (Scree) type also was described by DeVelice et al. (1986) in northern New Mexico.

***Pseudotsuga menziesii*/*Festuca arizonica* habitat type**
(PSME/FEAR; Douglas-fir/Arizona fescue)

This habitat type is found throughout the study area at moderate to high elevations (fig. 29). We sampled it in the Magdalena, San Mateo, and White Mountains in all three National Forests.

Vegetation.—This is another type described by Moir and Ludwig (1979). *Pseudotsuga menziesii* is usually dominant in all size classes. *Pinus strobiformis* and *Pinus ponderosa* occasionally are codominant. *Pseudotsuga menziesii* regeneration is usually moderate to abundant (20–490 stems per acre or 49–1,211 stems per ha). *Abies concolor* is not important in the stand. Shrubs (primarily *Holodiscus dumosus*) are subordinate to grasses, with less than 3% coverage. Grasses with 1% to 52% cover usually dominate the undergrowth; *Festuca arizonica* is usually the dominant grass, but *Bromus ciliatus*, *Muhlenbergia montana*, and other grasses often are present. *Bromus ciliatus* dominates under trees, with *Festuca arizonica*, *Muhlenbergia montana*, and *Poa fendleriana* in openings. *Muhlenbergia virescens* usually is absent, but may have 1% coverage in the New Mexico portion of the study area.

Physical setting.—Our plots were on ridges and upper and middle slopes from 9,250 to 10,200 feet (2,819 to 3,108 m) elevation. All aspects were represented except northeast, and slope gradients varied from 15% to 55%. This type is extensive on warm upper slopes, and is closely related to the PSME/BRCI HT.

Adjacent habitat types.—Both higher and lower elevations may support the PSME/BRCI HT. Similarly, phases of the PSME/QUGA HT also are found adjacent to this type. *Quercus gambelii* is dominant on rocky ridgetops.

Discussion.—Grass fires tend to reduce the density of conifer saplings and maintain grass cover in this type. The grazing value of this type would be high wherever slope steepness and distance to water are not limiting.

***Pseudotsuga menziesii*/Bromus ciliatus habitat type (PSME/BRCI; Douglas-fir/fringed brome)**

The PSME/BRCI HT is found in the Magdalena, San Mateo, and Mogollon Mountains in the Cibola and Gila National Forests, New Mexico.

Vegetation.—*Pseudotsuga menziesii* dominates both the overstory and the regeneration understory (fig. 30); *Pinus strobiformis*, or the hybrid *Pinus strobiformis* x *flexilis*, may be codominant and have low to moderate regeneration in late seral stands. *Abies concolor* is unimportant and only occasionally present. A distinguishing feature of this habitat type is the diverse and extremely



Figure 30.—*Pseudotsuga menziesii*/Bromus ciliatus habitat type. Grassy Mountain Lookout, San Mateo Mountains, 9,860 feet (3,005 m) elevation. *Pseudotsuga menziesii* dominates the overstory and the grassy undergrowth is extremely luxuriant. The type lies at the cold, wet extreme of the *Pseudotsuga menziesii* series environmental gradient.

luxuriant herbaceous undergrowth dominated by grasses. Total herb cover averages about 75%, but often exceeds 100%. The only constant undergrowth species is *Bromus ciliatus*, but other dominants frequently found are *Festuca arizonica*, *Poa fendleriana*, *Carex foenea*, *Achillea millefolium*, *Erigeron eximius*, *Haplopappus parryi*, and *Thalictrum fendleri*. Shrubs may or may not be conspicuous; the principal species, when present, are *Acer glabrum* and *Ribes pinetorum*. There are many minor or subordinate species, but *Berberis repens*, *Quercus gambelii*, *Rubus parviflorus*, *Vaccinium myrtillus*, and *Muhlenbergia virescens* were absent in our plots.

Physical setting.—This is basically a habitat type of deep, well-watered soils (such as Udic Haploborolls and Udic Argiborolls) on gentle upper slopes and broad ridgetops, mostly between 9,280 and 10,100 feet (2,828 and 3,078 m). We believe that the soil temperature regime is very near the cryic-frigid boundary, with the diurnal temperature range extended during the growing season because of lower nighttime temperatures caused by high reradiation or cold air convection. The more exposed sites contain trees with numerous, large limbs and heights less than about 50 feet (15.2 m), suggesting high evaporative demands and open growing conditions.

Adjacent habitat types.—*Picea engelmannii* and *Abies lasiocarpa* forests occur on slightly colder microsites; ABCO/ACGL or PSME/QUGA HT's occur on warmer microsites. Where cold air flows down gentle intermittent stream courses on cumelic soils, the ABCO/EREX HT can be encountered below the PSME/BRCI HT at an elevation as low as 8,500 feet (2,591 m). Small grassy parks with *Bromus ciliatus*, *Festuca arizonica*, and *Muhlenbergia montana* sometimes border the PSME/BRCI HT. Where rapid topographic changes occur, grassy *Pinus ponderosa* types may adjoin the PSME/BRCI HT.

Discussion.—Because of its limited area and for the reasons described below, this is not an important commercial forest. Some stands are logged because of the high volumes of old-growth *Pseudotsuga menziesii*. Mostly, this habitat type occurs in wilderness areas or on ridge crests where logging activities would have an adverse visual impact. Furthermore, growth in many stands appears only marginal. Herbaceous competition can be expected to hinder regeneration of *Pseudotsuga menziesii*, and low temperatures will most likely reduce annual growth rates. Windy sites probably have slow timber growth rates and pose severe regeneration problems. Closed, fully stocked stands may take centuries to develop under natural conditions.

There is evidence of occasional grass fires, but their frequency is unknown. On sheltered sites, such as draws, *Populus tremuloides* is an important seral species.

The PSME/BRCI HT provides ample forage for both wildlife and livestock. Heavy livestock use decreases *Festuca arizonica* and favors such species as *Achillea millefolium*, *Artemisia ludoviciana*, *Oxalis* spp., *Dugaldia hoopesii*, *Iris missouriensis*, *Pteridium aquilinum*, and *Poa pratensis*. The type is a known nesting area for band-tailed pigeons. We observed evidence of browsing activity by deer and rabbit on *Pseudotsuga menziesii* seedlings

in our plots, probably adversely affecting regeneration growth and survival. Also, we observed sites in this habitat type where grass fires killed saplings in thickets, possibly creating gaps in the age-class distribution of trees.

This habitat type is closely related to several other mixed conifer types with well-expressed herbaceous undergrowths. It resembles the ABCO/ACGL HT except for the much more luxuriant herbaceous undergrowth and poor representation of *Abies* as a climax species. Finally, the PSME/BRCI HT somewhat resembles ridgetop and windy site *Pinus flexilis* and *P. aristata* stands of northern New Mexico and Colorado (Marr 1961). However, the deep, mollic soils of the PSME/BRCI HT contrast sharply with the drier, more shallow, more stony, and often entisolic soils of these northern pine habitat types. Because of these various differences compared with related habitat types, we have concluded that the PSME/BRCI HT is a distinctive type at the cold and wet extreme of the *Pseudotsuga menziesii* series.

***Pseudotsuga menziesii*/Quercus gambelii habitat type (PSME/QUGA; Douglas-fir/Gambel oak)**

Both the typic and *Muhlenbergia virescens* phases of this habitat type are widely distributed throughout the entire study area (fig. 31). The *Festuca arizonica* phase is represented mostly in the Magdalena District of the Cibola National Forest, but it may be more widespread.

Vegetation.—*Pseudotsuga menziesii* or *Pinus ponderosa* is dominant. *Pseudotsuga menziesii* reproduction is

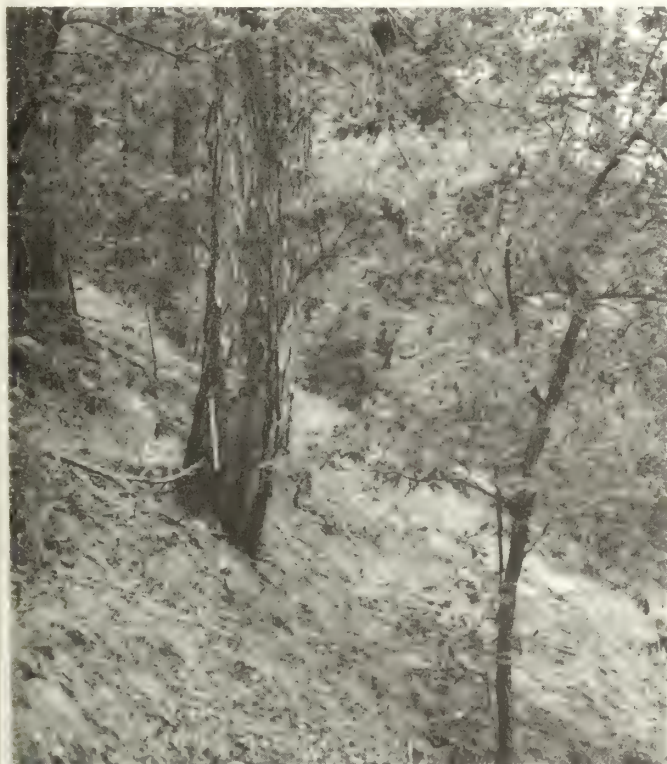


Figure 31.—*Pseudotsuga menziesii*/Quercus gambelii habitat type, typic phase; Russell Canyon, Gallo Mountains, 7,000 feet (2,133 m) elevation. This type occurs over a wide elevational range, often on thin or rocky soils, with cobbly or fractured parent materials.

more abundant in the typic phase, but sometimes not in other phases. *Abies concolor* is absent or unimportant in the stand. Shrubs, including *Quercus gambelii*, are equal to or exceed grass or forb coverage.

In the *Festuca arizonica* phase, *Festuca arizonica* dominates the herbaceous layer. *Muhlenbergia virescens* dominates in the *Muhlenbergia virescens* phase. *Poa fendleriana* is dominant or codominant in the *Quercus gambelii* phase.

Physical setting.—The habitat type is found between 6,500 and 9,650 feet (1,981 and 2,941 m) elevation on moderate to steep slopes (19% to 81%). Sites vary from lower slopes and rocky breaks at lower elevations to upper slopes and ridgetops above 8,000 feet (2,438 m). Soils vary, but often are shallow, with cobbly texture and fractured bedrock that provide pathways for root growth.

Adjacent habitat types.—Moister sites supported *Abies concolor*, *Picea pungens*, and *Populus angustifolia* types, and other *Pseudotsuga menziesii* types. Drier sites included the PIPO/MUVI HT and the PIPO/QUGA HT, MULO phase. Dry, rocky areas supported the PIPO/QUGA HT.

Discussion.—The PSME/QUGA HT has been described by Alexander et al. (1984a, 1984b, 1986), Youngblood and Mauk (1985), and DeVelice et al. (1986).

Under some conditions, the PSME/QUGA HT can occur adjacent to, and on sites drier than, the PIPO/QUGR HT. In these situations, dwarf mistletoe (*Arceuthobium* spp.) infection often was severe—infections were heavy at lower elevations and lighter at higher elevations. Severe ground fires often occurred 40 to 100 years before this study and may have increased oak coverage. Sites often were poorly rated for timber growth. Although *Pseudotsuga menziesii* regenerates easily, initial survival of regeneration may be a problem.

Big game sign was abundant in this type. In the *Festuca arizonica* phase, forbs showed an affinity to the *Pinus ponderosa*-grass types of Arizona, with such species as *Artemisia ludoviciana*, *Arenaria lanuginosa*, *Bahia dissecta*, and *Commelina* spp. sometimes present. The *Festuca arizonica* phase appeared to be typical of sites which support sparse timber stands, and probably exhibit low growth potential. Distance to water and slope steepness may restrict its utility for grazing. Stands in the PSME/QUGA HT have much structural vertical diversity, and tend to support a variety of bird species.

***Pseudotsuga menziesii*/Muhlenbergia virescens habitat type (PSME/MUVI; Douglas-fir/screwleaf muhly)**

We found the PSME/MUVI HT in the Mogollon Mountains and the Black Range, and on Elk Mountain in the Gila National Forest; it was also in the San Mateo Mountains, Cibola National Forest.

Vegetation.—Overstories in our plots were dominated by *Pinus ponderosa*, with *Pseudotsuga menziesii* or *Pinus strobiformis* often subdominant. *Pseudotsuga menziesii* regeneration was moderate to heavy (30–1,170 stems per acre or 74–2,891 stems per ha). *Abies concolor* was accidental or minor. *Picea pungens* and *Juniperus deppeana* were present in some plots, and *Populus tremuloides* oc-

asionally was a minor seral tree. Grass coverage (2–45%), with *Muhlenbergia virescens* dominant, equalled or was greater than forb coverage (trace to 12%), and exceeded shrub coverage (fig. 32). Plants that were absent included most tall shrubs and *Berberis repens*, *Quercus hypoleucoides*, *Q. rugosa*, *Symphoricarpos oreophilus*, *Vaccinium myrtillus*, *Erigeron eximius*, and *Fragaria americana*.

Physical setting.—Our plots occurred from ridgetops to lower slope positions that varied in steepness from 2% to 58% and occupied all but northeast aspects; elevations ranged between 7,880 and 9,400 feet (2,401 and 2,865 m). At lower elevations, this type was found on middle to upper slopes on northerly exposures.

Adjacent habitat types.—Moister and lower sites supported stands of *Picea pungens* and the ABCO/EREX HT. North slopes on deeper soils supported stands in the ABCO/QUGA HT. Drier sites supported the PIPO/MUVI-FEAR HT, and rocky ridgetops supported the PSME/ARUV HT. *Populus tremuloides* clones had a *Pteridium aquilinum*-*Muhlenbergia virescens* undergrowth, with some tall *Robinia neomexicana* plants. The PSME/QUGA HT occurred on deeper, more gravelly soils in some areas than did the PSME/MUVI HT. However, the PSME/MUVI HT also occurred occasionally on gravelly soils. It sometimes intergrades toward the PSME/QUGA HT, MUVI phase, with coverage of *Quercus gambelii* as high as 3%. It also integrades toward the ABCO/MUVI HT, but *Pseudotsuga menziesii* regeneration and grasses can exclude *Abies concolor* from the site in the PSME/MUVI HT.

Discussion.—Herbaceous cover in openings in the PSME/MUVI HT can reach 70%. More northerly slopes have more litter and less *Muhlenbergia virescens*, which is absent from tree thickets.

Some spruce budworm activity was observed on reproduction in this type.



Figure 32.—*Pseudotsuga menziesii*/*Muhlenbergia virescens* habitat type. Grass coverage in this type exceeds shrub coverage, and equals or exceeds forb coverage. The habitat type is found from 7,880 to 9,400 feet (2,401 to 2,865 m) elevation and on all aspects.



Figure 33.—*Pseudotsuga menziesii*/*Muhlenbergia montana* habitat type. San Mateo Mountains, 7,710 feet (2,350 m) elevation. This widely distributed grassy type often is dominated by *Muhlenbergia montana*, usually with other grass indicator species absent.

***Pseudotsuga menziesii*/*Muhlenbergia montana* habitat type**
(PSME/MUMO; Douglas-fir/mountain muhly)

The type was found throughout the study area. Most of our plots were in the San Mateo Mountains, Cibola National Forest, but the type also was sampled in the Blue Mountains, Apache National Forest, and Tularosa Mountains, Gila National Forest.

Vegetation.—Either *Pinus ponderosa* or *Pseudotsuga menziesii* may dominate a stand, but *P. menziesii* clearly is regenerating. *Pinus strobiformis*, *Pinus edulis*, *Juniperus deppeana*, and *J. scopulorum* occasionally are present, while *Abies concolor* is infrequent. Grasses, with 8–35% cover, usually dominate shrubs, and always dominate forbs (fig. 33). *Muhlenbergia virescens* usually is absent, but if not, *M. montana* dominates. Forbs are highly variable, but always sparse, with 6% or less cover. Shrubs have a trace to 10% cover. Species frequently found include *Quercus gambelii*, *Poa fendleriana*, *Artemisia carruthii*, *Erigeron platyphyllus*, *Geranium caespitosum*, and *Lithospermum multiflorum*. *Muhlenbergia rigens* and *Bouteloua gracilis* occasionally are present in small amounts. Species not found in this type include *Acer glabrum*, *Arctostaphylos uva-ursi*, *Berberis repens*, *Quercus rugosa*, *Festuca arizonica*, *F. sororia*, *Trisetum montanum*, *Erigeron eximius*, *Fragaria americana*, *Pteridium aquilinum*, and *Viola canadensis*.

Physical setting.—We found this type on all sideslope positions and in streamside settings. Slopes varied between 2% and 60%, mostly with southerly and westerly aspects. Elevations ranged from 7,540 to 9,750 feet (2,298 to 2,971 m). Some plots were on rocky, eroded, depleted soil. At lower elevations, soils were deeper and sandy.

Adjacent habitat types.—Moister sites supported the ABCO/QUGA HT. Drier sites supported the PIPO/MUMO HT. Habitat types found on adjacent ridgetops were the ABCO/ACGL, ABCO/Sparse, and PIPO/BOGR. Often, these habitat types at higher elevations were interspersed with fire-induced chaparral stands containing such species as *Cercocarpus montanus*, *Pinus edulis*, *Yucca baccata*, *Juniperus deppeana*, *Quercus grisea*, and *Muhlenbergia rigens*. Lower elevation sites supported the ABCO/MUVI and PSME/MUVI HT's. *Holodiscus dumosus* and *Quercus gambelii* increased on rocky areas, while meadows were grassy, with *Carex rossii* having about 30% coverage.

Discussion.—Grazing that occurs consistently during the same season causes successional changes in this type, the nature of which depends on the season when grazing occurs. Improper grazing can result in an undergrowth that is dominated by unpalatable forbs. Occasional, large, solitary oaks are den trees for wildlife, and are important food sources for turkey, deer, elk, bear, and songbirds. If wildlife values are to be sustained or enhanced, such trees should be maintained in the stand.

***Pseudotsuga menziesii*/Quercus hypoleucoides habitat type**
(PSME/QUHY; Douglas-fir/silverleaf oak)

The PSME/QUHY HT was sampled only in the Glenwood Ranger District of the Gila National Forest, on the south and west slopes of the Mogollon Mountains (fig. 34). It also occurs south of the Mogollon Rim in Arizona and in the Black Range in New Mexico.

Vegetation.—This is a climax type of mixed *Pinus ponderosa* and *Pseudotsuga menziesii*, with shrubs strongly dominant in the undergrowth (15% to 93%



Figure 34.—*Pseudotsuga menziesii*/Quercus hypoleucoides habitat type. Kings Crown, Mogollon Mountains, 7,880 feet (2,401 m) elevation. At climax, a mixture of shrubs, *Pinus ponderosa*, and *Pseudotsuga menziesii* dominate this warm, dry type.

coverage). Either *Quercus rugosa* or *Q. hypoleucoides* is dominant, but other shrubs often are present. Grasses and forbs have less than 10% coverage. Indicators of this type include a mixture of some of the following: *Agave* spp., *Echinocereus* spp., *Nolina microcarpa*, *Opuntia* spp., *Quercus rugosa*, *Q. hypoleucoides*, *Muhlenbergia longiligula*, and *M. monticola*. The herb layer usually is poorly represented, but occasional forbs include *Haplopappus parryi*, *Lithospermum multiflorum*, *Pseudocymopterus montanus*, and *Senecio neomexicanus*.

Physical setting.—This is a warm, dry type. It occurs on ridges and upper slopes from about 7,420 to 8,640 feet (2,261 to 2,633 m) and down to 6,920 feet (2,109 m) on middle and lower slopes. We found it only on southerly slopes of 37% to 85%.

Adjacent habitat types.—Adjacent types include those associated with canyon-bottom riparian sites. North and west slopes adjacent to the PSME/QUHY HT support stands of *Abies concolor* and *Abies concolor*-*Pseudotsuga menziesii* mixtures. South slopes support mixed chaparral-juniper woodland.

Discussion.—We considered the PSME/QUHY HT as climax vegetation because any further successional development would require changes in accumulated litter and soil organic matter content. Such changes could take centuries on these dry, erosion-prone sites. Ecologists who disregard time may prefer to identify this habitat type as a persistent seral community or a fire disclimax. Both *Pseudotsuga menziesii* and *Pinus ponderosa* are climax components. *Quercus rugosa* and *Q. hypoleucoides* are more common on rocky outcrops. There is more *Pinus ponderosa* on alluvial areas.

Dwarf mistletoe (*Arceuthobium* spp.) in this type infected *Pseudotsuga menziesii* moderately to heavily, and varied in intensity on *Pinus ponderosa*. *Pinus ponderosa* may be susceptible to fungal attacks in this type. Timber site quality is extremely poor. *Pinus ponderosa* and *Pseudotsuga menziesii* reach 45 to 55 feet (13.7 to 16.8 m) in height. Most trees over 200 years old had dead tops. Sites are steep and soils easily erodible, and as a consequence, logging could cause considerable damage. The habitat type supports little timber volume, and obtaining regeneration after logging may be a potentially severe problem. The sites are important deer habitat, and probably support large numbers of cavity-nesting birds.

Pinus ponderosa Series

***Pinus ponderosa*/Muhlenbergia virescens habitat type**
(PIPO/MUVI; ponderosa pine/screwleaf muhly)

This type occurs throughout the study area on all suitable sites (fig. 35).

Vegetation.—*Pinus ponderosa* is the dominant tree. *Abies concolor* and *Pseudotsuga menziesii* are absent or accidental—*P. menziesii* regeneration is less than 30 per acre (74 per ha). The undergrowth is dominated by *Muhlenbergia virescens*, and *Festuca arizonica* is absent.

Forbs are sparse, usually with less than 1% cover for individual species. Shrub coverage may equal that of grass.

We recognized a *Quercus gambelii* phase (more than 1% *Quercus gambelii*), which has a tendency to include tree species other than those found in the *Muhlenbergia virescens* phase. New Mexico stands tend to support more *Pinus edulis* and *Juniperus deppeana* than do stands in Arizona.

Physical setting.—The type occurred on all aspects between 7,760 and 8,700 feet (2,365 and 2,651 m). We found the type on all slope positions from alluvial benches to upper slopes.

Adjacent habitat types.—The PIPO/MUVI HT adjoins mesic *Pinus ponderosa* types in addition to stands with various combinations of *Pseudotsuga menziesii*, *Picea pungens*, and *Abies concolor*. Adjacent, moister sites supported PSME/QUGA, PIPU/FEAR, PSME/MUVI, and ABCO/QUGA HT's.

Discussion.—*Muhlenbergia virescens* seemed to occur on drier sites in the Gila and Cibola National Forests than in the Apache National Forest and farther west in Arizona. Repeated light surface fires were typical in this type, and evidence of a crown fire more than 150 years ago was observed on some plots. This is one of the most productive timber and forage types in the *Pinus ponderosa* series. *Poa compressa*, *Sitanion hystrix*, and *Iris missouriensis* increase under grazing. *Muhlenbergia virescens* was less abundant on flat alluvial sites. *Pinus ponderosa* seedlings were always present, sometimes with as many as 110 per acre (272 per ha). Turkeys, band-tailed pigeons, western tanagers (*Piranga ludoviciana*), western bluebirds (*Sialia mexicana*), and pygmy nuthatches (*Sitta pygmaea*) were observed in this type, attesting to its wildlife value. The mast and diversity provided by *Quercus gambelii* are partly responsible, and perpetuation of tree-sized oaks is important for wildlife species.



Figure 35.—*Pinus ponderosa*/*Muhlenbergia virescens* habitat type, *Quercus gambelii* phase. Kerr Lookout, Tularosa Mountains, 8,600 feet (2,621 m) elevation. *Muhlenbergia virescens* seems to occur on drier sites in the Gila National Forest than it does farther west and north.



Figure 36.—*Pinus ponderosa*/*Muhlenbergia virescens*-*Festuca arizonica* habitat type, typical phase. Iron Creek Mesa, Mogollon Mountains, 8,280 feet (2,523 m) elevation. This habitat type is identified by equal dominance of the two grasses for which the type is named.

***Pinus ponderosa*/*Muhlenbergia virescens*-*Festuca arizonica* habitat type**
(PIPO/MUVI-FEAR; ponderosa pine/screwleaf muhly-Arizona fescue)

This type appears to be concentrated in the White and Blue Mountains of Arizona and adjacent New Mexico areas. However, it also was found in the Gila Wilderness on Iron Creek Mesa and near Snow Lake outside the wilderness area.

Vegetation.—Stands consist of climax *Pinus ponderosa* with *Abies concolor* and *Pseudotsuga menziesii* absent or accidental. The undergrowth is characteristically grassy, with both *Muhlenbergia virescens* and *Festuca arizonica* represented (fig. 36). *Quercus gambelii* has 1% to 3% coverage (less than grasses) in the *Quercus gambelii* phase, and less coverage in the other phases. The *Bouteloua gracilis* phase is characterized by *B. gracilis* as a natural component. *Juniperus deppeana* and *Pinus edulis* also may be present. The typical phase lacks *Bouteloua gracilis*, and more *Pinus strobiformis* and *Pseudotsuga menziesii* may be present than in other phases.

Physical setting.—The PIPO/MUVI-FEAR HT occurs between 8,000 and 8,720 feet (2,438 and 2,657 m) elevation. All aspects and slopes up to 45% are represented. The typic phase usually occurs on gentle slopes along drainages, lakes, broad saddles, and flat, high-elevation mesas.

Adjacent habitat types.—This habitat type is near the wet end of the moisture gradient typical of the *Pinus ponderosa* series, but adjacent drier sites can support pinyon-juniper vegetation. Grassy mixed conifer and *Pseudotsuga menziesii* habitat types border it on north slopes and at higher elevations. Drainages on north-facing slopes may support *Picea pungens* habitat types. Although the PIPO/MUVI-FEAR HT is a separate type locally and is not a transition between the PIPO/FEAR and PIPO/MUVI HT's, from a broad geographical perspective it may be a climatically influenced transi-

tion between the PIPO/FEAR HT of northern Arizona and the PIPO/MUVI HT of southwestern New Mexico.

Discussion.—In this type, *Muhlenbergia virescens* has the greatest coverage on cobbly soils. Coverage usually is less than 1% under a well developed tree canopy. *Quercus gambelii* grows on steeper slopes, and increases upslope, whereas *Festuca arizonica* increases on lower slopes. Swales and other sites with good moisture relationships in this type are the best timber sites, but some soil scarification may be needed to prepare a seedbed for tree regeneration.

Livestock induced changes in undergrowth composition tend to confuse identification of the typic and *Bouteloua gracilis* phases because *Bouteloua gracilis* invades the typic phase as a result of grazing.

Hanks et al. (1983) described the *Bouteloua gracilis* phase as a seral stage of the PIPO/MUVI-FEAR HT and called it a community type. We added no additional plots to those sampled by Hanks et al. (1983), but better acquaintance with New Mexico plant communities as a result of this study has convinced us that this is a valid phase, and not a seral stage. However, many of the typical plants in the phase can increase greatly in density as a result of disturbance.

***Pinus ponderosa*/Quercus grisea habitat type (PIPO/QUGR; ponderosa pine/gray oak)**

The PIPO/QUGR HT is widely distributed in all parts of the study area (fig. 37). The *Muhlenbergia longiligula* phase occurs in the San Francisco, Mogollon, Blue, and Saliz Mountains, and probably in other areas in the central and southwestern part of the Gila and Apache National Forests. The *Muhlenbergia montana* phase is more typical of the northeastern part of the study area in the Mogollon and San Mateo Mountains. No predominating phase has been identified as typical throughout the range of the habitat type.

Vegetation.—*Pinus ponderosa*, *P. edulis*, and *Juniperus deppeana* are co-climax species. *Pseudotsuga menziesii* may be a minor climax component, but often is absent.



Figure 37.—*Pinus ponderosa*/Quercus grisea habitat type, *Muhlenbergia longiligula* phase. Near Blue Ranger Station, San Francisco Mountains, 8,040 feet (2,450 m). *Pinus ponderosa*, *P. edulis*, and *Juniperus* spp., accompanied by *Quercus grisea* and other oaks, form a canopy over a grassy undergrowth.

Quercus grisea and other oaks dominate the undergrowth and become trees in seral stages. Grasses form an important component in a rather sparse herbaceous community. *Muhlenbergia longiligula*, *M. virescens*, or *M. montana* usually dominate. Normally, either *Muhlenbergia montana* or *M. longiligula* will be absent; but if both are present, their relative dominance determines whether the site is in the *M. longiligula* phase or the *M. montana* phase of the habitat type. *Festuca arizonica*, *Muhlenbergia dubia*, *M. emersleyi*, *Piptochaetium fimbriatum*, and *Stipa* spp. are absent.

Physical setting.—Our plots were located on ridgetops to lower slopes varying from 15% to 59%. All aspects were represented, from southeast slopes at higher elevations to northwest at lower elevations. Elevations varied from 6,160 to 8,840 feet (1,877 to 2,694 m). Soils usually were shallow, rocky, gravelly, or cobbly.

Adjacent habitat types.—Moister sites support various *Pinus ponderosa* and *Pseudotsuga menziesii* habitat types with *Quercus gambelii*, *Festuca arizonica*, *Muhlenbergia montana* or *M. virescens* undergrowths. Riparian canyon bottoms adjacent to this type often support the PIPU/EREX HT, with a narrow band of the PIPO/QUGA HT between it and the PIPO/QUGR HT. Drier sites support pinyon-juniper with *Bouteloua gracilis* and *Cercocarpus montanus* undergrowths.

Discussion.—Sites on which the habitat type is found are poor quality for timber production. Rocky areas support increasing densities of *Cercocarpus montanus*, *Juniperus deppeana*, *Bouteloua gracilis*, *Muhlenbergia montana*, with abundant *Pinus edulis* and *Quercus grisea*. Improper grazing increases *Artemisia ludoviciana* and decreases *Muhlenbergia montana*.

***Pinus ponderosa*/Rockland habitat type (PIPO/Rockland; ponderosa pine/rockland)**

This type was found at widely scattered locations in the Apache and Gila National Forests, but probably occurs wherever suitable rocky sites exist high in the *Pinus ponderosa* zone (fig. 38).



Figure 38.—*Pinus ponderosa*/Rockland habitat type. Lower Steeple Canyon, San Francisco Mountains, 6,080 feet (1,853 m) elevation. The type is extremely poor for timber production and probably would normally not be harvested.

Vegetation.—*Pinus ponderosa* and sometimes *Pseudotsuga menziesii* and *Pinus strobiformis* are widely scattered. Regeneration often is sparse. The undergrowth is variable, but sparse. Shrubs typically are stunted, with only a trace of cover, but several species may be present. *Quercus grisea* may have measurable coverage, and *Muhlenbergia montana* usually is present. Many other grasses may be present, including *Muhlenbergia virescens*, *Festuca arizonica*, *Agropyron arizonicum*, and *Bromus* spp. Typically, many forbs are present, with low coverage. Grass cover is 9% to 13%, while forb cover varies from a trace to 12%.

Physical setting.—Our plots were on mid to lower slopes with gradients of 48% to 60%, and on southerly aspects from 8,300 to 8,750 feet (2,530 to 2,666 m) elevation. They were found on bare rockland sites, with exposed rock comprising 5–90% of the surface. Soil depth to bedrock is less than 4 inches (10 cm). Exposed roots and measurements on root crowns provided evidence of erosion during the last 200 years, with approximately 8 inches (20 cm) of soil lost.

Adjacent habitat types.—The PIPO/Rockland HT adjoined *Picea pungens* streamside types below. The PIPO/MUVI-FAER HT was found upslope on drier sites, but with deeper soils.

Discussion.—These are extremely poor sites for timber and normally would not be harvested. Regeneration of trees is difficult and many decades could pass before a new stand is established. The sites may be scenic, but appear of little value for other resources. Alexander et al. (1986) described this type in the Cibola National Forest.

***Pinus ponderosa*/Festuca arizonica habitat type (PIPO/FAER; ponderosa pine/Arizona fescue)**

The PIPO/FAER HT is widespread in our study area (fig. 39). We found it in most Ranger Districts, and only in the Clifton District of the Apache National Forest was the acreage minor. The habitat type occurs in almost all mountains, along the upper drainages of the Blue River, and within high valleys and plateaus. It is common in the White Mountains, and along forested slopes adjoining the San Augustin Plains.

Vegetation.—Typically, these stands are composed entirely of *Pinus ponderosa*. Occasionally, *Juniperus scopulorum* or *J. deppeana* appear. Near the drier edge of the habitat type, especially in New Mexico, *Pinus edulis* is a minor seral tree. Shrubs, if present, are sparse in the typical phase. The undergrowth is grassy (12% to 69% cover) with *Festuca arizonica* and *Muhlenbergia montana* dominant or codominant. *Stipa pringlei* may dominate also, possibly after fire.

We identified three phases in the study area. Sites with more than 5% shrub cover, including *Quercus gambelii*, are in the *Quercus gambelii* phase. The *Festuca arizonica* (typic) phase lacks *Bouteloua gracilis* and shrubs except in trace amounts. The *Bouteloua gracilis* phase contains at least 1% *Bouteloua gracilis* in the undergrowth, with



Figure 39.—*Pinus ponderosa*/Festuca arizonica habitat type, Festuca arizonica phase. Iron Creek Canyon, Mogollon Mountains, 8,040 feet (2,450 m) elevation. Phases of this habitat type provide valuable range, wildlife, and timber resources throughout the Southwest.

shrubs less than 5%. In addition, some plots in the *Bouteloua gracilis* phase were distinguished by the presence of *Lycurus phleoides*, which is normally associated with dry sites.

Physical setting.—The PIPO/FAER HT is found typically on gentle slopes of all aspects between 7,880 and 8,114 feet (2,401 and 2,473 m) elevation. The *Bouteloua gracilis* phase can occur at lower elevations to about 7,400 feet (2,256 m). The *Quercus gambelii* phase can be found on steeper slopes or where soils appear more stony. These phases can occur on shallow soils, but usually soils are deep or moderately deep. The soil moisture regime is toward the wet end of ustic, and soil temperatures are near the frigid zone (USDA Forest Service 1983).

Adjacent habitat types.—The PIPO/FAER HT represents a middle range within the vegetation gradient in the *Pinus ponderosa* series. It usually is found adjacent to other *Pinus ponderosa* habitat types. However, the PSME/QUGA HT and the mixed conifer and *Pinus edulis*-*Juniperus* spp. types also may be adjacent where site characteristics change rapidly. Where soils are more stony, or on north-facing steeper slopes, the PIPO/QUGA HT can be found. The PIPO/FAER HT commonly borders open grassy parks dominated at climax by *Festuca arizonica*, *Muhlenbergia montana*, and associated herbs. *Bouteloua gracilis* parks are found on flat areas, with fine textured alluvial soils, adjacent to the *Bouteloua gracilis* phase.

Discussion.—This is an important and major habitat type in the Southwest⁹ (Hanks et al. 1983, DeVelice et al. 1986). The major changes in the present study from the description by Hanks et al. (1983) of the PIPO/FEAR HT are the increased presence of *Pinus edulis*, *Juniperus* spp., and *Lycurus phleoides* in the *Bouteloua gracilis* phase. *Juniperus* spp. and *Pinus edulis* trees seem to be found more frequently on drier sites and as one proceeds easterly through the range of the type. *Juniperus deppeana* may increase following fire or cutting. Timber productivity is mostly moderate or high, depending upon soil properties. Fires have been important historically, with surface fires recurring about every 4 to 8 years. These fires usually covered large areas, often 3,000 acres (1,214 ha) or more (Swetnam and Dieterich 1985). Herbage productivity is inversely related to tree density or overstory dominance (Clary 1975, Hall 1983). This habitat type constitutes a major range for livestock. The undergrowth is rich in cool season grasses, so that pine-bunchgrass ranges are important summer pasturage. On overused ranges, *Bouteloua gracilis* increases (as does *Poa pratensis* on wetter microsites), and *Festuca arizonica* and *Muhlenbergia montana* both decline.

In the *Bouteloua gracilis* phase, *Oxytropis lambertii* also appeared to increase following excessive grazing. Decreasers were *Festuca arizonica*, *Muhlenbergia montana*, and *Andropogon* spp. *Muhlenbergia repens* appeared to invade. *Fallugia paradoxa* and *Chrysothamnus nauseosus* were observed along a heavily grazed wash. Logging disturbance favored *Agropyron smithii*, *Bouteloua gracilis*, *Erigeron flagellaris*, *Lappula* spp., and annual *Lupinus* spp. In the *Quercus gambelii* phase, grazing increased *Achillea millefolium* and *Erigeron* spp., decreased grasses, and expanded the area of rubble pavement.

Range condition classes have been described by Arnold (1950, 1955), Talbot (1957), Smith (1967), Bostick,¹⁰ Costello and Schwan,¹¹ and by the pine-bunchgrass scorecards.¹² Additional information on the reaction of phases of this habitat type to grazing are found in Hanks et al. (1983). Range management practices have been reviewed by Clary (1975) and Currie (1975).

All phases are important wildlife habitat, especially the *Quercus gambelii* phase because of its greater diversity, potential den sites, and mast production. The *Quercus gambelii* phase probably produces less forage and timber than the typic phase, and care is needed to avoid unnecessary soil disturbance.

The typical gentle slopes, accessibility, and high productivity of this habitat type are conducive to overuse.

⁹U.S. Department of Agriculture, Forest Service. 1981. *The plant associations of Region 2*. 152 p. Region 2, Denver, Colo. (Mimeo.)

¹⁰Bostick, V. B. 1947. *Principles for judging condition and trend of southwestern woodland ranges*. 66 p. Southwestern Forest and Range Experiment Station and Region 3, U.S. Forest Service. (Mimeo.)

¹¹Costello, David, F., and H. E. Schwan. 1946. *Conditions and trends on ponderosa pine ranges in Colorado*. 33 p. USDA Forest Service. (Mimeo.)

¹²Range Vegetation Score Card Handbook, 2209.21a, R-3. Apache National Forest Score Card 015, Pine Bunchgrass and Associated Grassland. USDA Forest Service, Southwestern Region.



Figure 40.—*Pinus ponderosa*/*Muhlenbergia montana* habitat type. Middle Fork, Gila River Trail, Mogollon Mountains, 7,880 feet (2,401 m) elevation. *Pinus ponderosa*, *P. edulis*, and *Juniperus deppeana* and a grassy undergrowth, lacking indicator species other than *Muhlenbergia montana*, are characteristic of this moderately dry habitat type.

***Pinus ponderosa*/*Muhlenbergia montana* habitat type (PIPO/MUMO; ponderosa pine/mountain muhly)**

The PIPO/MUMO HT is widely distributed in all three National Forests studied (fig. 40). The type appears to be best expressed in the southern Rocky Mountains (DeVelice et al. 1986), and was not recognized by Hanks et al. (1983) in Arizona, although we suggest below that it may occur there.

Vegetation.—*Pinus ponderosa*, *P. edulis*, and *Juniperus deppeana* usually form a tree stand, with grasses dominating the undergrowth. *Pseudotsuga menziesii*, *Juniperus monosperma*, *Quercus grisea*, and *Q. gambelii* sometimes are present, and shrubs may dominate grasses with as much as 25% cover. This type differs from the PIPO/BOGR HT in having more *Muhlenbergia montana* and *Quercus grisea*, with *Q. gambelii* often present. *Bouteloua gracilis* and *Sitanion hystrix* also are present. *Muhlenbergia virescens* is absent or present only with trace amounts. *Festuca arizonica*, *Muhlenbergia dubia*, *M. emersleyi*, and *Stipa* spp. are absent.

Physical setting.—Our plots occurred on ridges to lower slopes, with gradients from 4% to 37%. All aspects were represented between 7,140 and 8,200 feet (2,176 and 2,499 m) elevation.

Adjacent habitat types.—The PIPO/MUMO HT adjoins many other grassy types depending on the nature of the adjacent site. The relationship begins in the *Pinus edulis*-*Juniperus* spp. series, extends through several *Pinus ponderosa* and *Pseudotsuga menziesii* types, and ends with *Picea pungens* types on moister sites.

Discussion.—North slopes had more *Quercus gambelii* and less *Muhlenbergia* spp. Rock outcrops also had more *Quercus gambelii*, and fewer grasses grew where *Pinus ponderosa* litter occurred. Eroded or disturbed areas had more *Blepharoneuron tricholepis*, *Bouteloua gracilis*, *Poa fendleriana*, *Sitanion hystrix*, *Muhlenbergia minutissima*, *Artemisia carruthii*, *Erigeron* spp., and annual *Lupinus*

spp. Such areas may be the result of mechanical disturbance, improper grazing, or intense rodent burrowing activity. *Muhlenbergia rigens* may be locally dominant because of grazing disturbance. Our plots may have lost mid-grasses, such as *Stipa pringlei*, because of a long history of grazing.

Some plots that Hanks et al. (1983) placed in their PIPO/POFE community type probably belong in this type (see discussion of the PIPO/QUGA HT). A gradient appears to exist from the PIPO/BOGR HT, typic phase in northern Arizona (Hanks et al. 1983) to the PIPO/MUMO HT in this study and then north through New Mexico (Alexander et al. 1986; DeVelice et al. 1986) into Colorado and to Utah (Youngblood and Mauk, 1985). Descriptions of the PIPO/MUMO HT vary considerably between these areas and different phase designations probably should be assigned.

***Pinus ponderosa*/Quercus gambelii habitat type (PIPO/QUGA; ponderosa pine/Gambel oak)**

This is a widespread type, occurring in all National Forests in this study, but more commonly in New Mexico than in Arizona.

Vegetation.—*Pinus ponderosa* is dominant, with *Pseudotsuga menziesii* absent or minor. *Abies concolor* is absent. *Pinus edulis* and *Juniperus* spp. may be present. *Quercus gambelii* is present with more than 5% cover, either as a shrub or tree or both (fig. 41). The herbaceous layer is grassy, dominated by *Bromus* spp., *Muhlenbergia longiligula*, *Poa fendleriana*, *Sitanion hystrix*, or *Carex* spp.

We recognized two phases; the *Quercus gambelii* (typic) phase is slightly less grassy than the *Muhlenbergia longiligula* phase. *Muhlenbergia longiligula* always is present in the *Muhlenbergia longiligula* phase, and is absent in the *Quercus gambelii* phase.

Physical setting.—This type occurs on ridges, slopes, and benches from 6,000 to 8,560 feet (1,828 to 2,609 m). The *Muhlenbergia longiligula* phase is usually below



Figure 41.—*Pinus ponderosa*/Quercus gambelii habitat type, typic phase. Upper West Fork, Pueblo Creek, San Francisco Mountains, 7,040 feet (2,145 m) elevation. *Pinus ponderosa*, *Quercus gambelii*, and a grassy-herbaceous layer identify this habitat type.

7,000 feet (2,134 m), and the typic phase is on northerly slopes above 7,000 feet. Sometimes this type appears to occupy depauperate sites following erosion from unknown causes, possibly early historic grazing or fire, or a high natural rate of geologic erosion (north slopes of Brushy Mountains). At this stage in history, the type represents an edaphic climax on those sites. Hanks et al. (1983) also found the PIPO/POFE community type on areas where soil properties had been altered (see discussion below). Elsewhere, the type can occur on shallow soils where the site approaches rockland conditions.

Adjacent habitat types.—Adjacent sites support types ranging from chaparral and *Pinus edulis*-*Juniperus* spp. woodlands through *Pinus ponderosa* types to the PSME/QUGA HT.

Discussion.—After reviewing our data, the data of Hanks et al. (1983), and results from the Lincoln, Cibola, Carson, and Santa Fe National Forests (Alexander et al. 1984a, 1986; DeVelice et al. 1986), the authors have concluded that several of the plots that Hanks et al. placed in a PIPO/POFE community type actually belong in a PIPO/QUGA HT, QUGA phase. Hanks et al. did not recognize a distinct habitat type because their study area was at the edge of the range of this type. Therefore, we propose to change the name of their PIPO/POFE community type to PIPO/QUGA HT, QUGA phase, to make it more consistent with developing information in the rest of Arizona and New Mexico. DeVelice et al. (1986) recognized this type, as did Alexander et al. (1984a, 1986), and Youngblood and Mauk (1985). Data from all of these studies indicates considerable geographical variation within the typic phase. Thus, the typic phase may not be ecologically equivalent in different geographical areas.

The PIPO/QUGA HT varies from low to moderate timber productivity, with shallow, rocky soils that often are easily damaged if mistreated. *Bouteloua gracilis*, *Achillea millefolium*, and *Artemisia* spp. may increase with disturbance, while *Muhlenbergia montana* may decrease. On eroding microsites, *Pinus ponderosa* seedlings were found growing in clumps of *Quercus gambelii* where litter and soil accumulated.

***Pinus ponderosa*/Bouteloua gracilis habitat type (PIPO/BOGR; ponderosa pine/blue grama)**

The PIPO/BOGR HT, *Pinus edulis* phase of this habitat type (Hanks et al. 1983) was found throughout the Apache and Gila National Forests in lower elevation *Pinus ponderosa* forests (fig. 42). It undoubtedly also is present in the Magdalena District of the Cibola National Forest. The *Vitis arizonica* phase was found in the southern portion of the Apache National Forest in the Big Lue Mountains. The typical phase (Hanks et al. 1983) was not found in our area.

Vegetation.—*Pinus ponderosa* is the canopy dominant, but *Juniperus deppeana* and *Pinus edulis* usually are more abundant in small sizes. In many New Mexico stands, the woodland representative *Juniperus deppeana* replaces *Pinus edulis* in the Hanks et al. (1983) key and

in descriptions for the *P. edulis* phase in northern Arizona. *Quercus grisea* usually is present, but tree-form *Q. gambelii* is found only occasionally. Grasses have greater cover than shrubs. *Bouteloua gracilis* is always dominant or codominant in the undergrowth.

The *Vitis arizonica* phase is a riparian type along intermittent streams, with *Pinus ponderosa*, *Bouteloua gracilis*, and *Quercus* spp. found in combination with a low, but significant, coverage of vines and shrubs such as *Vitis arizonica*, *Lonicera albiflora*, *Prunus* spp., *Rhamnus betulaeifolia*, and *Rhus glabra*. Such plants are found at this elevation only where water is augmented from off-site sources.

Physical setting.—Our plots were in all topographic positions. Slopes varied from 1% to 34%, and elevations from 5,720 to 8,040 feet (1,743 to 2,450 m). Soils included those that were shallow and rocky, and others that were deep, sandy loam alluviums with few coarse fragments. The *Vitis arizonica* phase was on deep, subirrigated soils (Typic Ustifluvents), possibly with a relatively persistent high water table.

Adjacent habitat types.—This is the driest *Pinus ponderosa* type that we identified. Drier sites support *Pinus edulis*-*Juniperus* spp. woodlands and *Cercocarpus montanus*, *Quercus grisea*, and grassland communities. Moist sites support the PSME/QUGA HT and nearly any of the *Pinus ponderosa* habitat types. Thinner, rockier soils support woodlands with *Cercocarpus montanus*.

Discussion.—Most of our plots in this habitat type fit the description of the PIPO/BOGR HT, PIED phase of Hanks et al. (1983), except that *Quercus grisea* was not found in northern Arizona stands. However, we attached no ecological significance to the addition of *Q. grisea*, and stands containing it were not considered to be different phases. The *Pinus edulis* phase also seems to be similar to the *Pinus ponderosa*/*Bouteloua gracilis* HT, *Schizachyrium scoparium* phase of DeVelice, et al. (1986).

The demarcation between this type and the PIPO/FEAR HT, BOGR phase, is arbitrary. We used site differences and changes in vegetation gradients to make the distinction.



Figure 42.—*Pinus ponderosa*/*Bouteloua gracilis* habitat type, *Pinus edulis* phase. Steeple Canyon, east of Blue Ranger Station, 7,240 feet (2,206 m) elevation. This is a very common habitat type at the dry end of the *Pinus ponderosa* series environmental gradient.

Bouteloua curtipendula, *Pinus edulis*, and *Juniperus* spp. increase on westerly and southerly exposures. *Quercus gambelii* also increases on middle and lower slopes with north-facing aspects. *Poa fendleriana* occurs in patches on deeper soils. Disturbance by rodents under trees stimulates the growth of shrubs and forbs such as *Ribes* spp., *Sambucus* spp., *Argemone* spp., *Artemisia carruthii*, and *Chenopodium album*. Patches of *Andropogon gerardi* and *Poa* spp. grow under clumps of *Pinus ponderosa*. *Quercus grisea* and *Muhlenbergia longiligula* disappear on deep, sandy soils in gentle draws, where the type grades into a stand more typical of the *Pinus edulis* phase.

Grazing increases *Artemisia ludoviciana*, *Asclepias* spp., *Calliandra humilis*, *Chenopodium graveolens*, *Cirsium* spp., *Dalea* spp., *Erigeron flagellaris*, *Eriogonum alatum*, *Hymenoxys* spp., *Lupinus* spp., *Potentilla crinita*, *Aristida arizonica*, *A. fendleriana*, *Bouteloua gracilis*, and *Sitanion hystrix*. Grazing decreases *Andropogon cirratus*, *Bouteloua curtipendula*, *Piptochaetium fimbriatum*, and *Setaria* spp.

Timber productivity is low in all phases. However, the *Vitis arizonica* phase is an important riparian community because it provides water, food, and cover to wildlife that inhabit adjacent types during part of their daily or seasonal routines. It also is important for livestock forage production. However, there probably is a tendency for livestock to rest in the shade provided by the canopy, eventually causing damage to the undergrowth and preventing tree regeneration.

***Pinus ponderosa*/Arctostaphylos pungens community type (PIPO/ARPU; ponderosa pine-pointleaf manzanita)**

This community type is found on the slopes of the Mogollon Rim throughout the Apache National Forest (fig. 43). As indicated by Hanks et al. (1983), stands best exemplifying it are found somewhere in central Arizona, south of the Mogollon Rim.

Vegetation.—This community type includes *Pinus ponderosa*-*Arctostaphylos* spp. or *Pinus ponderosa*-mixed chaparral communities which lack the dominant brushy life form of *Quercus gambelii* characteristic of the New Mexico *Pinus ponderosa* stands with shrubby undergrowth. *Quercus gambelii* in tree form, however, can be an important component in this community type. *Q. emoryi*, *Q. arizonica*, *Q. turbinella*, and *Arctostaphylos pungens* are characteristic.

Physical setting.—Our plots occurred on ridgetops between 6,850 and 7,600 feet (2,088 and 2,316 m) elevation on northerly aspects with 20% to 65% slopes. We know from Hanks et al. (1983) that the *Pinus ponderosa*-*Arctostaphylos pungens* community type occurs on relatively level sites and on other aspects as well.

Adjacent habitat types.—This community type usually occurs adjacent to chaparral or *Pinus edulis*-*Juniperus* spp. communities. It grows on steep slopes below the Mogollon Rim, but is a fire-disclimax community on top of the Rim. It may occur adjacent to other *Pinus ponderosa* or mixed conifer types.



Figure 43.—*Pinus ponderosa*-*Arctostaphylos pungens* community type. Mogollon Rim area, 7,000 feet (2,130 m) elevation. This undefined group of associations reaches its characteristic development south of the Mogollon Rim where it currently is being studied.

Discussion.—Hanks et al. (1983) described this type. Habitat types within this community will be described in subsequent studies.¹³ General features of the community type are described in the Terrestrial Ecosystem Survey (U.S. Forest Service 1983).

Timber productivity is low. Any disturbance in communities of this subseries will increase brush coverage to the detriment of timber, wildlife, and livestock values. Properly controlled fire at appropriate frequencies may be a useful tool in management, but wildfire or indiscriminant burning can increase the brush problem.

***Populus angustifolia* Series**

The *Populus angustifolia* series consists of riparian (streamside or floodplain) sites at lower elevations in the coniferous forests of the Southwest (fig. 44). We sampled the series in the Mogollon and San Francisco Mountains of the Gila and Apache National Forests. The series is widespread and scattered, but encompasses a relatively small total acreage. Yet, its value and level of interest to the public are high.

Vegetation.—The distinguishing characteristics of this series are the presence of riparian trees such as *Acer negundo*, *Alnus oblongifolia*, *Juglans major*, *Populus angustifolia*, and low-elevation gymnosperms such as *Pinus ponderosa*, *P. edulis*, *Pseudotsuga menziesii*, *Juniperus deppeana*, and *J. scopulorum*. While conifers may have more stems per acre than deciduous trees, the size and crown spread of the latter often create canopy

¹³Plant Association Classifications (Forest Habitat Types) for the Coronado, Prescott, and Tonto National Forests. Rocky Mountain Forest and Range Experiment Station, Contract 28-K3-307 with New Mexico State University.



Figure 44.—*Populus angustifolia* series. Lower Mineral Creek, Mogollon Mountains, 6,320 feet (1,926 m) elevation. This is a group of highly variable riparian habitat types that are extremely important for wildlife.

dominance. Shrubs usually are subordinate to grasses and forbs. Grasses usually dominate forbs until *Pseudotsuga menziesii* begins to appear in the canopy, when forbs become more important.

Physical setting.—This series was found between 6,200 and 7,710 feet (1,889 and 2,350 m) elevation, usually between about 1.5 and 6.5 feet (0.5 and 2 m) above the permanent water level on alluvial terraces. The plant community is highly influenced by physical site factors, including the watercourse, watershed size and shape, elevation, aspect, and onsite and upstream parent material. These, in turn, influence such things as soil moisture, depth of alluvium, and periodicity and severity of flooding.

Adjacent habitat types.—The *Populus angustifolia* series exists in riparian stringers through *Pseudotsuga menziesii*, *Pinus ponderosa*, *Pinus edulis*-*Juniperus* spp., and chaparral communities.

Discussion.—This series is dependent on permanent water. Some potential habitat types within the series are most likely adapted to torrential floods which scarify the soil surface, creating a disclimax undergrowth community composed of annuals and rapidly-invading or deep-rooted persistent perennials with the ability to sprout from roots. Tree seedlings typical of these flood-adapted types have slender, flexible stems.

Communities change rapidly with differences in elevation. We were unable to find enough replicates of each habitat type to adequately subdivide the series.

Comments regarding grazing, logging, and wildlife values discussed in the ABCO/ACGR and ABCO/JUMA HT's, and the *Vitis arizonica* phase of the PIPO/BOGR HT, also apply to the *Populus angustifolia* series.

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Appendix A. Keys to the Forest Series and Habitat Types on the Apache, Gila, and Cibola (Magdalena District) National Forests

The keys to identify forest series and habitat types were developed from mature, minimally disturbed forest stands, because those that are young, or severely disturbed by grazing, logging, fire, recreation or other activities are difficult to classify. Instead of attempting to identify a disturbed stand through the key, the nearest mature stand occupying a similar site should be identified, applying the habitat type so identified to the disturbed stand. Be careful to avoid edge effects and ecotones. The habitat type of moderately disturbed sites often can be identified using these keys by inferring future tree dominance from those that are successfully reproducing and by searching carefully in undisturbed microsites for undergrowth species.

This section illustrates how the keys are used by identifying a hypothetical stand, which in this example, is an *Abies lasiocarpa*/*Lathyrus arizonicus* habitat type. Choose a location within the stand that you judge to be occupied by the typical vegetation. At this location, proceed with the following steps:

1. Estimate and record, by species, the relative number of trees—abundant, common, or sparse—in each of three diameter (breast height) classes: under 2 inches (5.1 cm), 2 to 10 inches (5.1 to 25.4 cm), and over 10 inches (25.4 cm).

An example of your notes, using the first letter of the category indicating relative tree number, or a dash for no entry, would appear as follows:

Species ^a	Under 2 inches	2 to 10 inches	Over 10 inches
ABLA	c	a	s
PSME	c	—	c
ABCO	—	—	c
PIST	s	s	c

^aAbbreviations for habitat types employ a shorthand form of scientific notation using the first two letters of the genus and species names.

2. Estimate and record canopy coverage of dominant shrubs, graminoids, and forbs, separating shrubs into two height categories—low shrubs, under about breast height (4.5 feet or 1.37 meters), and tall shrubs which exceed that height. For example:

Tall shrubs—

SASC	3%
ACGL	1%

Low shrubs—

HODU	4%
SYOR	1%

Graminoids—

BRCI	3%
KOCR	2%

Forbs—

SEWO	1%
------	----

Also, consider the following questions. Is the undergrowth generally shrubby? Is it mostly dominated by herbs (forbs and graminoids)? Are shrubs, forbs, or graminoids about equal in cover? Which life form (shrubs, forbs, or graminoids) shows the greatest crown cover?

3. Include in the list drawn up for Step 2 the relative abundance of indicator plants shown in various keys.¹⁴ In this example, assume that *Erigeron eximius* covers less than 1%.

Terminology used to describe relative abundance in keys and habitat type descriptions is as follows.

Scarce (0 to 1%), common (>1%), poorly represented (0 to 5%), well represented (>5%), and abundant (>25%) were previously defined by Steele et al. (1981). Luxuriant represents coverage >50%. Minor or unimportant signifies that the plant does not contribute much to community composition. Accidental means that the species is not normally found in similar examples of the habitat type; its presence may be the result of seeding from adjacent types, for example.

4. Refer to the keys. As indicated earlier, the hypothetical stand in this example is identified as an ABLA/LAAR HT.
5. Compare the characteristics of the stand with the written description of the habitat type that was determined from the keys.

If the stand characteristics do not satisfactorily match the habitat type description, one or more of the following procedures may help to determine the correct habitat type:

1. Walk through the stand again, carefully reassessing its characteristics, and revising your estimates of coverage or density if necessary. Be alert for indicator plants that may have been overlooked the first time through the stand. Also, consider the patchiness of the vegetation, such as small openings or pole thickets to be a normal part of the vegetational structure, adjusting your estimates of plant cover accordingly.
2. If the selection of alternatives in the key is doubtful, follow both options at questionable decision points.
3. Compare the existing stand characteristics with all aspects of the written description, not just the vegetation portion. Questions that remain after such a comparison sometimes may be resolved by referring to the plant association tables, appendix D.
4. If necessary, measure the coverage or density of all species in a sample plot of the stand. If repeated attempts fail to identify a stand after exhausting all alternative procedures, you may have to draw the conclusion that either keys or descriptions are inadequate for the existing situation, the stand is transitional along a successional or environmental gradient, or a new plant association has been found.
5. Rely on the written description and association table, rather than the keys alone, to confirm the identity of a given habitat type.

¹⁴A list of indicator species for riparian sites is shown in appendix E.

KEYS

Key A—Key to Series and Riparian Types

1. *Picea pungens* present, neither accidental nor seral ----- 2
1. *Picea pungens* absent, accidental, or seral ----- 3
 2. *Picea engelmannii* plus *Abies lasiocarpa* less than 10 inches (25.4 cm) d.b.h. more than three times as abundant as *Picea pungens* less than 10 inches d.b.h. ----- 3
 2. *Picea engelmannii* plus *Abies lasiocarpa* less than 10 inches (25.4 cm) d.b.h. less than three times as abundant as *Picea pungens* of the same size ----- KEY C
3. *Picea engelmannii* or *Abies lasiocarpa* common; combined *Picea engelmannii* and *Abies lasiocarpa* 2 to 10 inches (5.1 to 25.4 cm) d.b.h. are more numerous than *Abies concolor* 2 to 10 inches d.b.h., usually indicating *Abies concolor* is seral, or else *Senecio cardamine* present ----- KEY B
3. *Senecio cardamine* absent. *Picea engelmannii* and *Abies lasiocarpa* both absent, or if either is present, then the total number of stems 2 to 10 inches (5.1 to 25.4 cm) d.b.h. is fewer than *Abies concolor* ----- 4
 4. Obligate riparian trees or shrubs present (*Acer negundo*, *Salix* spp., *Alnus oblongifolia*, *Populus angustifolia*, *Acer grandidentatum*, *Juglans major*) ----- 7
 4. Obligate riparian trees and shrubs absent ----- 5
5. *Abies concolor* present, neither accidental nor seral^a ----- KEY D
5. *Abies concolor* absent or accidental ----- 6
 6. *Pseudotsuga menziesii* present, not accidental^b ----- KEY E
 6. *Pseudotsuga menziesii* absent or accidental ----- KEY F
7. *Acer grandidentatum* dominant or codominant in undergrowth -----

----- *Abies concolor*/*Acer grandidentatum* habitat type
7. *Acer grandidentatum* minor or absent ----- 8
 8. *Populus angustifolia* or *Alnus oblongifolia* present ----- *Populus angustifolia* Series
 8. *Populus angustifolia* and *Alnus oblongifolia* absent ----- 9
9. *Abies concolor*, *Juglans major* present, *Bouteloua gracilis* absent -----

----- *Abies concolor*/*Juglans major* habitat type
9. *Abies concolor* absent, *Pinus ponderosa* and *Bouteloua gracilis* present on low-elevation riparian sites -
----- *Pinus ponderosa*/*Bouteloua gracilis* habitat type, *Vitis arizonica* phase.

Key B—*Picea engelmannii* and *Abies lasiocarpa* Series

Picea pungens absent (occasionally seral); 2 to 10 inch (5.1 to 25.4 cm) d.b.h. *Picea engelmannii* and *Abies lasiocarpa* together more numerous than 2 to 10 inch d.b.h. *Abies concolor*.

1. Herb plus low shrub cover less than 5% ----- *Picea engelmannii*/Moss habitat type
1. Herb plus low shrub cover 5% or greater ----- 2
 2. *Vaccinium myrtillus* common (at least 1% cover), often dominant ----- 3
 2. *Vaccinium myrtillus* scarce, often absent ----- 5
3. *Rubus parviflorus* common, usually more than 2% cover -----

----- *Abies lasiocarpa*/*Vaccinium myrtillus* habitat type, *Rubus parviflorus* Phase
3. *Rubus parviflorus* scarce or absent (rarely to 4% cover, but then much less common than *Vaccinium myrtillus*) 4
 4. *Abies lasiocarpa* absent or accidental. ----- *Picea engelmannii*/*Vaccinium myrtillus* habitat type
 4. *Abies lasiocarpa* a component of the climax community -----

----- *Abies lasiocarpa*/*Vaccinium myrtillus* habitat type, typic phase
5. Scree (loose rock) soils with shrub cover exceeding herbaceous cover -----

----- *Abies lasiocarpa*/*Holodiscus dumosus* (Scree) habitat type
5. Soils otherwise or shrub cover less than herbaceous cover ----- 6
 6. *Senecio cardamine* present ----- 7
 6. *Senecio cardamine* absent ----- 9
7. *Abies lasiocarpa* minor, seral, or accidental -----

----- *Picea engelmannii*/*Senecio cardamine* habitat type, *Abies concolor* phase
7. *Abies lasiocarpa* a climax component ----- 8
 8. *Erigeron eximius* with 1% or more coverage, or *Rubus parviflorus* with more than 2% coverage ----- 9
 8. *Erigeron eximius* absent or only trace amounts present and *Rubus parviflorus* with 2% or less coverage ----- *Picea engelmannii*/*Senecio cardamine* habitat type, *Abies lasiocarpa* phase
9. *Abies lasiocarpa* accidental, not climax ----- *Picea engelmannii*/*Erigeron eximius* habitat type
9. *Abies lasiocarpa* a climax component ----- 10
 10. *Erigeron eximius* with 1% coverage, usually more ----- *Abies lasiocarpa*/*Erigeron eximius* habitat type.

10. *Erigeron eximius* absent or with less than 1% coverage ----- 11
11. *Rubus parviflorus* with 1% or more coverage ----- *Abies lasiocarpa*/*Rubus parviflorus* habitat type
11. *Rubus parviflorus* absent or with less than 1% coverage -----
----- *Abies lasiocarpa*/*Lathyrus arizonicus* habitat type

Key C—*Picea pungens* Series

Picea pungens present as a climax component, not accidental or seral. *Picea pungens* reproduction^c usually present. If absent, see Key B.

1. *Senecio cardamine* present usually in patches ----- *Picea pungens*/*Senecio cardamine* habitat type
1. *Senecio cardamine* absent or minor ----- 2
 2. Obligate riparian trees or shrubs (*Salix bebbiana*, *Alnus* spp., and others) present. *Poa pratensis* with at least 5% cover; alluvial streamside sites. ----- *Picea pungens*/*Poa pratensis* habitat type
 2. Obligate riparian trees or shrubs absent. *Poa pratensis* minor or absent. ----- 3
3. *Picea pungens* less than 10 inches (25.4 cm) d.b.h. fewer than twice the number of *Picea engelmannii* plus *Abies lasiocarpa* in the same size class ----- KEY B
3. *Picea pungens* less than 10 inches (25.4 cm) d.b.h. more than twice as abundant as *Picea engelmannii* plus *Abies lasiocarpa* of the same size class ----- 4
 4. Forbs dominant, forb coverage about 1.5 to 30 times graminoid coverage -----
----- *Picea pungens*/*Erigeron eximius* habitat type
 4. Graminoids visually dominant; forb cover not more than about 1.8 times grass coverage. *Erigeron eximius* usually 1% coverage or less ----- 5
5. Bunchgrasses and caespitose sedges well represented, coverage usually exceeding that of rhizomatous sedges with single-stem growth form ----- 6
5. Rhizomatous sedges characterize the appearance of the herbaceous layer -----
----- *Picea pungens*/*Carex foenea* habitat type
6. *Abies concolor* dominates over *Picea pungens* in all size classes -----
----- *Abies concolor*/*Festuca arizonica* habitat type, *Poa fendleriana* phase
6. *Picea pungens* more abundant than *Abies concolor* -----
----- *Picea pungens*/*Festuca arizonica* habitat type

Key D—*Abies concolor* Series

Abies concolor or *Pseudotsuga menziesii* are the dominant climax overstory trees.

1. Obligate riparian plants present ----- Key A
1. Obligate riparian plants absent ----- 2
 2. Cover of herbs and shrubs together less than about 8% (sometimes more if one shrub species has up to 10% cover); usually not more than two undergrowth species with cover over 2%. *Picea engelmannii* sometimes present and not accidental ----- *Abies concolor*/Sparse habitat type
 2. Cover of combined herbs and low shrubs greater than about 8%, usually more than two undergrowth species have cover over 2%; *Picea engelmannii* absent or accidental ----- 3
3. Undergrowth, excluding tall shrubs, essentially herbaceous ----- 7
3. Shrub cover about equal to or greater than herb cover ----- 4
 4. *Quercus gambelii* absent or poorly represented ----- 5
 4. *Quercus gambelii* dominant or at least well represented. -----
----- *Abies concolor*/*Quercus gambelii* habitat type
5. *Acer glabrum* common ----- *Abies concolor*/*Acer glabrum* habitat type
5. *Acer glabrum* absent or scarce ----- 6
 6. *Robinia neomexicana* dominant or common ----- *Abies concolor*/*Robinia neomexicana* habitat type
 6. *Robinia neomexicana* absent or scarce ----- *Abies concolor*/*Holodiscus dumosus* (Scree) habitat type
7. *Bromus ciliatus* the most prominent grass; *Erigeron eximius* with at least 1% cover. Herbaceous cover luxuriant, usually near or exceeding 100%. ----- *Abies concolor*/*Erigeron eximius* habitat type^d
7. Other grasses dominant; herbaceous cover less, *Erigeron eximius* absent or with 2% or less coverage ----- 8
 8. *Muhlenbergia virescens* the dominant grass, or at least codominant with other grasses -----
----- *Abies concolor*/*Muhlenbergia virescens* habitat type
 8. Other grasses dominant or codominant ----- 9
9. *Festuca arizonica* dominant or codominant ----- *Abies concolor*/*Festuca arizonica* habitat type
9. Other grasses dominant ----- 10
 10. *Poa fendleriana* dominant or codominant -----
----- *Abies concolor*/*Festuca arizonica* habitat type *Poa fendleriana* phase
10. *Bromus ciliatus* or *Agropyron arizonicum* dominant ----- *Abies concolor*/*Erigeron eximius* habitat type

Key E—*Pseudotsuga menziesii* Series

Pseudotsuga menziesii is the only climax dominant tree^a.

1. Herbaceous cover often luxuriant; *Bromus ciliatus* usually dominant; *Pinus ponderosa* absent or minor ----- *Pseudotsuga menziesii*/*Bromus ciliatus* habitat type
1. *Bromus ciliatus* less abundant than other grasses; *Pinus ponderosa* common or absent ----- 2
 2. *Quercus gambelii* with 5% or more coverage; other *Quercus* species with less than 10% coverage ----- *Pseudotsuga menziesii*/*Quercus gambelii* habitat type
 2. *Quercus gambelii* with less than 5% coverage or other *Quercus* species with more than 10% coverage ----- 3
3. *Arctostaphylos uva-ursi* in conspicuous mats (San Mateo Mountains) ----- *Pseudotsuga menziesii*/*Arctostaphylos uva-ursi* habitat type
3. *Arctostaphylos uva-ursi* absent ----- 4
 4. *Robinia neomexicana*, *Holodiscus dumosus*, *Symphoricarpos oreophilus* or other shrubs dominate on scree soils ----- *Pseudotsuga menziesii*/*Holodiscus dumosus* (Scree) habitat type
 4. Soils not scree; grasses or *Quercus* spp. well represented ----- 5
5. *Quercus* spp. well represented ----- 6
5. Grasses well represented, *Quercus* spp. absent or poorly represented ----- 7
 6. *Quercus hypoleucoides* present, usually common ----- *Pseudotsuga menziesii*/*Quercus hypoleucoides* habitat type
 6. *Quercus hypoleucoides* absent, *Quercus grisea* common ----- *Pinus ponderosa*/*Quercus grisea* habitat type
7. *Muhlenbergia virescens* dominant or codominant ----- *Pseudotsuga menziesii*/*Muhlenbergia virescens* habitat type
7. *Muhlenbergia virescens* minor or absent ----- 8
 8. *Muhlenbergia montana* or *Poa fendleriana* dominant or codominant; *Festuca arizonica* absent ----- *Pseudotsuga menziesii*/*Muhlenbergia montana* habitat type
 8. *Festuca arizonica* present, usually common ----- *Pseudotsuga menziesii*/*Festuca arizonica* habitat type

Key F—*Pinus ponderosa* Series

Abies concolor, *Pseudotsuga menziesii*, *Picea* spp., *Abies lasiocarpa* all are absent or accidental^b; *Pinus ponderosa* is the dominant tree.

1. Undergrowth dominated by chaparral typical of lower elevations, with *Garrya wrightii* or *Quercus turbinella* present, or *Q. rugosa* dominant among shrubs ----- *Pinus ponderosa*-*Arctostaphylos pungens* Community Type
1. *Garrya wrightii* and *Quercus turbinella* absent and *Q. rugosa* minor ----- 2
 2. Bedrock close to surface and much of it exposed. Small amounts of many grass and forb species present, with total undergrowth coverage less than 30%. Trees few, with poor growth. ----- *Pinus ponderosa*/Rockland habitat type
 2. Soil deeper, not a typical rockland site ----- 3
3. *Muhlenbergia virescens* important in the herbaceous layer, sometimes codominant with *M. montana*. *Festuca arizonica*, *Bouteloua gracilis*, *M. longiligula* absent or accidental; *Quercus grisea*, if present, with less coverage than the dominant grass ----- *Pinus ponderosa*/*Muhlenbergia virescens* habitat type
3. *Festuca arizonica*, *Muhlenbergia longiligula*, or *Bouteloua gracilis* present, or *M. virescens* absent or a minor component of the stand, or *Quercus grisea* with greater coverage than the dominant grasses ----- 4
 4. Both *Muhlenbergia virescens* and *Festuca arizonica* present ----- *Pinus ponderosa*/*Muhlenbergia virescens*-*Festuca arizonica* habitat type
 4. *Muhlenbergia virescens* or *Festuca arizonica* or both absent ----- 5
5. *Festuca arizonica* always present; *Festuca arizonica* and *Muhlenbergia montana* usually with more than 1% coverage; *Muhlenbergia virescens* absent ----- *Pinus ponderosa*/*Festuca arizonica* habitat type
5. *Festuca arizonica* absent or with less than 1% coverage, or *Muhlenbergia virescens* present ----- 6
 6. *Muhlenbergia montana* with 2% or greater coverage, usually dominating grasses; *Quercus grisea* absent or subordinate to other shrubs. *Quercus gambelii* with less than 10% coverage ----- *Pinus ponderosa*/*Muhlenbergia montana* habitat type
 6. *Muhlenbergia montana* with less than 2% cover, subordinate to other grasses, or *Quercus grisea* dominating shrubs, or *Quercus gambelii* with more than 10% cover ----- 7

7. *Bouteloua gracilis* or *Bouteloua curtipendula* dominant or codominant among grasses. *Pinus edulis* and *Juniperus* spp. often important components of the stand. *Quercus* spp. usually with less than 5% coverage ----- *Pinus ponderosa*/*Bouteloua gracilis* habitat type
7. *Bouteloua gracilis* and *Bouteloua curtipendula* subordinate to other grasses; oaks usually with 5% or more coverage ----- 8
8. *Quercus grisea* dominant among shrubs ----- *Pinus ponderosa*/*Quercus grisea* habitat type
8. *Quercus gambelii* dominant among shrubs ----- *Pinus ponderosa*/*Quercus gambelii* habitat type

^aStands that are actually in the *Pseudotsuga menziesii* series may be incorrectly keyed to the *Abies concolor* series if long, unnatural intervals between fires have resulted in invasion of *Abies concolor* in what naturally would be *Pseudotsuga menziesii* site.

^bStands that are actually in the *Pinus ponderosa* series may be incorrectly keyed to the *Pseudotsuga menziesii* series if long, unnatural intervals between fires have resulted in invasion of *Pseudotsuga menziesii* in what naturally would be a *Pinus ponderosa* site.

^cRegeneration and reproduction are used synonymously to denote trees less than 4.5 feet (1.37 m) tall.

^dPeriodic fires, low winter temperatures, and/or excessive snow cover may prevent *Abies concolor* seedlings from attaining maturity.

Appendix B. A list of plants observed in relatively undisturbed forest stands on the Apache, Gila, and Cibola (Magdalena District) National Forests and the number of plots in which the species was found

We sampled 394 plots and identified 491 plant species. See the methods section, under the heading "naming the types" for procedure used to determine synonymy.

Life Form and Species	Number of Plots ¹	Shrubs	
Trees		<i>Acer glabrum</i>	69
<i>Abies concolor</i>	154	<i>Acer grandidentatum</i>	5
<i>Abies lasiocarpa</i>	84	(<i>A. saccharum</i>)	
<i>Acer negundo</i>	7	<i>Alnus tenuifolia</i>	4
<i>Alnus oblongifolia</i>	10	<i>Amelanchier utahensis</i>	8
<i>Fraxinus pennsylvanica</i>	10	<i>Arctostaphylos pungens</i>	2
(<i>F. velutina</i>) ²		<i>Arctostaphylos uva-ursi</i>	4
<i>Juglans major</i>	7	<i>Baccharis thesioides</i>	1
<i>Juniperus deppeana</i>	63	<i>Berberis repens</i>	20
<i>Juniperus monosperma</i>	3	(<i>Mahonia repens</i>)	
<i>Juniperus osteosperma</i>	5	<i>Calliandra humilis</i>	15
(<i>J. utahensis</i>)		<i>Ceanothus fendleri</i>	45
<i>Juniperus scopulorum</i>	16	<i>Cercocarpus montanus</i>	35
<i>Picea engelmannii</i>	105	(<i>C. betuloides</i>)	
<i>Picea pungens</i>	66	<i>Chimaphila umbellata</i>	35
<i>Pinus discolor</i>	2	<i>Chrysothamnus nauseosus</i>	2
(<i>P. cembroides</i>)		<i>Cornus stolonifera</i>	6
<i>Pinus edulis</i>	81	(<i>Swida sericea</i>)	
<i>Pinus leiophylla</i>	2	<i>Dalea formosa</i>	1
<i>Pinus ponderosa</i>	249	<i>Dalea leporina</i>	1
<i>Pinus strobus</i>	201	<i>Fallugia paradoxa</i>	1
<i>Populus angustifolia</i>	7	<i>Fendlera rupicola</i>	8
<i>Populus tremuloides</i>	101	<i>Garrya wrightii</i>	8
<i>Pseudotsuga menziesii</i>	288	<i>Gutierrezia sarothrae</i>	2
<i>Quercus arizonica</i>	2	(<i>Xanthocephalum sarothrae</i>)	
<i>Quercus chrysolepis</i>	1	<i>Holodiscus dumosus</i>	58
(<i>Q. muhlenbergii</i>)		<i>Hymenoxys richardsonii</i>	11
<i>Quercus emoryi</i>	2	<i>Jamesia americana</i>	18
<i>Quercus gambelii</i>	274	<i>Juniperus communis</i>	34
<i>Quercus grisea</i>	58	<i>Linnaea borealis</i>	1
<i>Quercus hypoleucoides</i>	19	<i>Lonicera albiflora</i>	5

<i>Lonicera arizonica</i>	66	<i>Agrostis alba</i>	2
<i>Lonicera involucrata</i>	12	(<i>A. gigantea</i>)	
<i>Lonicera utahensis</i>	76	<i>Agrostis scabra</i>	7
<i>Nolina microcarpa</i>	3	<i>Andropogon</i> spp.	21
<i>Pachistima myrsinites</i>	39	<i>Andropogon cirratus</i>	4
<i>Parthenocissus vitacea</i>	4	(<i>Schizachyrium cirratum</i>)	
(<i>P. inserta</i>)		<i>Andropogon gerardi</i>	2
<i>Philadelphus</i> spp.	5	<i>Andropogon scoparius</i>	5
<i>Physocarpus monogynus</i>	38	(<i>Schizachyrium scoparium</i>)	
(<i>P. malvaceus</i>)		<i>Aristida</i> spp.	2
<i>Populus tremuloides</i>	121	<i>Aristida arizonica</i>	32
<i>Potentilla fruticosa</i>	3	<i>Aristida orcuttiana</i>	1
(<i>Pentaphylloides floribunda</i>)		<i>Aristida fendleriana</i>	1
<i>Prunus emarginata</i>	9	<i>Aristida wrightii</i>	1
<i>Prunus virginiana</i>	10	<i>Blepharoneuron tricholepis</i>	102
<i>Ptelea trifoliata</i>	5	<i>Bouteloua curtipendula</i>	8
<i>Quercus rugosa</i>	13	<i>Bouteloua gracilis</i>	57
<i>Quercus aff. turbinella</i>	1	<i>Bromus</i> spp.	71
<i>Quercus undulata</i>	0	<i>Bromus anomalous</i>	13
(<i>Q. gambelii</i> x <i>grisea</i>)		(<i>Bromopsis porteri</i>)	
<i>Rhamnus betulaefolia</i>	9	<i>Bromus carinatus</i>	5
<i>Rhus trilobata</i>	12	<i>Bromus ciliatus</i>	236
(<i>R. aromatica</i>)		(<i>B. richardsonii</i> ,	
<i>Rhus glabra</i>	2	<i>Bromopsis ciliata</i>)	
<i>Ribes</i> spp.	29	<i>Bromus frondosus</i>	8
<i>Ribes cereum</i>	17	(<i>Bromopsis frondosa</i>)	
<i>Ribes montigenum</i>	3	<i>Bromus inermis</i>	2
<i>Ribes pinetorum</i>	52	(<i>Bromopsis inermis</i>)	
<i>Ribes wolfii</i>	20	<i>Bromus japonicus</i>	1
<i>Robina neomexicana</i>	107	<i>Bromus lanatipes</i>	5
<i>Rosa</i> spp.	74	(<i>Bromopsis lanatipes</i>)	
<i>Rubus arizonensis</i>	2	<i>Bromus marginatus</i>	14
(<i>R. woodsii</i>)		(<i>Ceratochloa marginata</i>)	
<i>Rubus neomexicanus</i>	4	<i>Bromus orcuttianus</i>	1
<i>Rubus parviflorus</i>	81	<i>Calamagrostis canadensis</i>	1
<i>Rubus strigosus</i>	32	<i>Calamagrostis inexpansa</i>	3
(<i>R. idaeus</i> var. <i>strigosus</i>)		(<i>C. neglecta</i>)	
<i>Salix</i> spp.	4	<i>Carex</i> spp.	191
<i>Salix bebbiana</i>	1	<i>Carex aurea</i>	2
(<i>S. depressa</i>)		<i>Carex bella</i>	1
<i>Salix scouleriana</i>	49	<i>Carex festivella</i>	1
<i>Salix subcoerulea</i>	1	<i>Carex foenea</i>	88
(<i>S. drummondiana</i>)		<i>Carex geophila</i>	4
<i>Sambucus</i> spp.	17	<i>Carex lanuginosa</i>	1
<i>Shepherdia canadensis</i>	5	<i>Carex media</i>	1
<i>Sorbus dumosa</i>	12	(<i>C. norvegica</i> ssp. <i>stevenii</i>)	
<i>Symphoricarpos oreophilus</i>	60	<i>Carex microptera</i>	4
<i>Toxicodendron rydbergii</i>	11	<i>Carex occidentalis</i>	14
(<i>T. radicans</i> , <i>Rhus radicans</i>)		<i>Carex praegracilis</i>	1
<i>Vaccinium myrtillus</i>	33	<i>Carex rossii</i>	102
(<i>V. oreophilum</i>)		<i>Cyperus</i> spp.	2
<i>Vitis arizonica</i>	6	<i>Cyperus aristatus</i>	1
<i>Yucca baccata</i>	22	(<i>Cyperus inflexus</i>)	
<i>Yucca schottii</i>	1	<i>Cyperus rusbyi</i>	12
Graminoids		<i>Danthonia</i> spp.	1
<i>Agropyron</i> spp. (probably <i>A. smithii</i>)	5	<i>Danthonia californica</i>	1
<i>Agropyron arizonicum</i>	18	<i>Elymus glaucus</i>	3
<i>Agropyron trachycaulum</i>	4	<i>Festuca arizonica</i>	89
<i>Agrostis</i> spp.	4	<i>Festuca ovina</i>	1
		(<i>F. brachyphylla</i>)	
		<i>Festuca sororia</i>	23

<i>Festuca thurberi</i>	3	<i>Allium gooddingii</i>	2
<i>Glyceria elata</i>	4	<i>Allium kunthii</i>	2
<i>Glyceria grandis</i>	1	<i>Allium rhizomatum</i>	4
(<i>G. maxima</i> spp. <i>grandis</i>)		<i>Amaranthus</i> spp.	2
<i>Glyceria striata</i>	2	<i>Anaphalis margaritacea</i>	1
<i>Juncus interior</i>	1	<i>Androsace occidentalis</i>	3
(<i>J. tenuis</i>)		<i>Antennaria</i> spp.	16
<i>Juncus longistylis</i>	1	<i>Antennaria marginata</i>	41
<i>Koeleria nitida</i>	212	(<i>A. neglecta</i>)	
(<i>K. cristata</i> , <i>K. macrantha</i> , <i>K. pyramidata</i>)		<i>Antennaria parvifolia</i>	56
<i>Luzula parviflora</i>	3	(<i>A. aprica</i>)	
<i>Lycurus phleoides</i>	14	<i>Anthericum torreyi</i>	3
<i>Melica porteri</i>	6	<i>Apocynum</i> spp.	8
<i>Muhlenbergia longiligula</i>	27	<i>Aquilegia</i> spp.	5
<i>Muhlenbergia minutissima</i>	1	<i>Aquilegia chrysantha</i>	6
<i>Muhlenbergia montana</i>	110	<i>Aquilegia elegantula</i>	25
<i>Muhlenbergia monticola</i>	1	<i>Aquilegia triternata</i>	19
<i>Muhlenbergia pauciflora</i>	4	(<i>A. barnebyi</i>)	
<i>Muhlenbergia racemosa</i>	5	<i>Arabis</i> spp.	27
<i>Muhlenbergia repens</i>	1	<i>Arabis fendleri</i>	1
<i>Muhlenbergia rigens</i>	21	<i>Arenaria</i> spp.	15
<i>Muhlenbergia virescens</i>	129	<i>Arenaria lanuginosa</i>	23
<i>Muhlenbergia wrightii</i>	8	(<i>A. confusa</i> , <i>A. saxosa</i>)	
<i>Panicum bulbosum</i>	1	<i>Artemisia campestris</i> ssp. <i>pacifica</i>	9
<i>Phleum pratensis</i>	1	(<i>A. pacifica</i>)	
<i>Piptochaetium fimbriatum</i>	7	<i>Artemisia carruthii</i>	58
<i>Poa</i> spp.	1	<i>Artemisia dracunculus</i>	8
<i>Poa compressa</i>	3	(<i>A. dracunculoides</i>)	
<i>Poa fendleriana</i>	236	<i>Artemisia franserioides</i>	88
<i>Poa nervosa</i> var. <i>tracyi</i>	1	<i>Artemisia frigida</i>	4
(<i>P. traceyi</i> , <i>P. wheeleri</i>)		<i>Artemisia ludoviciana</i>	95
<i>Poa palustris</i>	2	<i>Asclepias</i> spp.	3
<i>Poa pratensis</i>	25	<i>Asclepias asperula</i>	1
<i>Schizachne purpurascens</i>	2	(<i>A. capricornu</i>)	
<i>Scirpus microcarpus</i>	3	<i>Asclepias speciosa</i>	1
(<i>S. microcarpa</i>)		<i>Asclepias tuberosa</i>	2
<i>Setaria geniculata</i>	5	<i>Aster</i> spp.	5
<i>Sitanion hystrix</i>	182	<i>Aster commutatus</i> ³	5
(<i>S. longifolium</i>)		(<i>A. falcatus</i>)	
<i>Sporobolus cryptandrus</i>	1	<i>Astragalus</i> spp.	30
<i>Stipa</i> spp.	1	<i>Astragalus cobrensis</i>	1
<i>Stipa pringlei</i>	16	<i>Astragalus egglestonii</i>	7
<i>Trisetum montanum</i>	49	<i>Astragalus gilensis</i>	27
(<i>T. spicatum</i> ssp. <i>montanum</i>)		<i>Astragalus humistratus</i>	11
		<i>Astragalus rusbyi</i>	2
		<i>Athyrium filix-femina</i>	2
Forbs		<i>Bahia dissecta</i>	38
<i>Achillea millefolium</i>	185	<i>Besseyia plantaginea</i>	1
(<i>A. lanulosa</i>)		<i>Bidens</i> spp.	6
<i>Aconitum columbianum</i>	3	<i>Bistorta bistortoides</i>	1
<i>Actaea rubra</i> ssp. <i>arguta</i>	15	(<i>Polygonum bistortoides</i>)	
(<i>A. arguta</i>)		<i>Brickellia</i> spp.	55
<i>Agastache pallidiflora</i>	16	<i>Brickellia brachyphylla</i>	1
<i>Agave parryi</i>	4	<i>Brickellia fendleri</i>	5
<i>Ageratina herbacea</i>	14	<i>Brickellia grandiflora</i>	6
(<i>Eupatorium herbaceum</i>)		<i>Calypso bulbosa</i>	5
<i>Agoseris aurantiaca</i>	7	<i>Campanula rotundifolia</i>	46
<i>Agrimonia striata</i>	7	<i>Cardamine cordifolia</i>	2
<i>Allium</i> spp.	4	<i>Castilleja</i> spp.	51
<i>Allium cernuum</i>	30	<i>Castilleja miniata</i>	3
		(<i>C. confusa</i>)	

<i>Cerastium</i> spp.	2	<i>Dryopteris filix-mas</i>	2
<i>Cerastium nutans</i>	4	<i>Dugaldia hoopesii</i>	64
<i>Cerastium brachypodum</i>	1	(<i>Helenium hoopesii</i>)	
(<i>C. nutans</i> var. <i>brachypodum</i>)		<i>Echinocereus</i> spp.	13
<i>Cerastium texanum</i>	2	(<i>Mammillaria</i> spp.)	
<i>Chaptalia alsophila</i>	17	<i>Epilobium adenocaulon</i>	3
<i>Cheilanthes</i> spp.	2	<i>Epilobium angustifolium</i>	39
(Some species synonymous with some <i>Notholaena</i> spp.)		(<i>Chamerion angustifolium</i>)	
<i>Cheilanthes fendleri</i>	2	<i>Equisetum</i> spp.	7
<i>Chenopodium</i> spp.	6	<i>Equisetum arvense</i>	1
<i>Chenopodium</i> aff. <i>album</i>	4	<i>Equisetum laevigatum</i>	2
<i>Chenopodium graveolens</i>	9	(<i>Hippochaete laevigata</i>)	
<i>Cicuta douglasii</i> ²	2	<i>Erigeron</i> spp.	17
(<i>C. maculata</i>)		<i>Erigeron concinnus</i>	2
<i>Circaea alpina</i>	5	<i>Erigeron delphinifolius</i>	38
<i>Cirsium</i> spp.	91	(<i>E. neomexicanus</i>)	
<i>Cirsium arizonicum</i>	7	<i>Erigeron divergens</i>	9
<i>Cirsium calcareum</i>	5	<i>Erigeron eximius</i>	125
(<i>C. pulchellum</i>)		(<i>E. superbus</i>)	
<i>Cirsium parryi</i>	10	<i>Erigeron flagellaris</i>	63
<i>Cirsium wheeleri</i>	4	<i>Erigeron formosissimus</i>	37
<i>Clematis ligusticifolia</i>	9	<i>Erigeron platyphyllus</i>	67
<i>Clematis pseudoalpina</i>	66	<i>Erigeron speciosus</i> var. <i>speciosus</i>	4
(<i>C. columbiana</i>)		<i>Eriogonum alatum</i>	42
<i>Cologania longifolia</i>	20	<i>Eriogonum hieracifolium</i>	1
(<i>C. angustifolia</i>)		<i>Eriogonum jamesii</i>	17
<i>Commelina dianthifolia</i>	19	<i>Eriogonum pharnaceoides</i>	1
<i>Conopholis mexicana</i>	6	<i>Eriogonum racemosum</i>	2
(<i>C. alpina</i>)		<i>Erysimum capitatum</i>	20
<i>Conyza schiedeana</i>	4	<i>Erythrocoma triflora</i>	1
<i>Corallorhiza</i> spp.	6	(<i>Geum triflorum</i>)	
<i>Corallorhiza maculata</i>	34	<i>Euphorbia</i> spp.	17
<i>Corallorhiza striata</i>	2	<i>Euphorbia chamaesula</i>	4
<i>Corallorhiza wisteriana</i>	2	<i>Euphorbia lurida</i>	4
<i>Coryphantha</i> spp.	1	<i>Euphorbia palmeri</i>	5
(Some species synonymous with some <i>Mammillaria</i> spp.)		<i>Euphorbia robusta</i>	1
<i>Cosmos bipinnatus</i>	2	<i>Fragaria americana</i>	88
(<i>C. parviflorus</i>)		(<i>F. bracteata</i> , <i>F. vesca</i>)	
<i>Crotalaria pumila</i>	1	<i>Fragaria ovalis</i>	165
<i>Cryptantha</i> spp.	1	(<i>F. virginiana</i> var. <i>glauca</i>)	
<i>Cryptantha jamesii</i>	11	<i>Gaillardia</i> spp.	1
<i>Cucurbita foetidissima</i>	1	<i>Galium</i> spp.	28
<i>Cystopteris fragilis</i>	36	<i>Galium fendleri</i>	28
<i>Dalea</i> spp.	1	<i>Galium mexicanum</i>	3
<i>Dalea filiformis</i>	3	(<i>G. asperimum</i>)	
<i>Dalea ordiae</i>	2	<i>Galium triflorum</i>	5
<i>Dalea polygonoides</i>	7	<i>Galium wrightii</i>	1
<i>Delphinium tenuisectum</i>	2	<i>Gaura hexandra</i>	9
<i>Descurainia</i> spp.	1	(<i>G. gracilis</i>)	
<i>Desmanthus cooleyi</i>	4	<i>Gentiana bigelovii</i>	5
<i>Desmodium</i> spp.	1	(<i>Pneumonanthe affinis</i>)	
<i>Desmodium</i> cf. <i>cinerascens</i>	1	<i>Gentianella amarella</i> ssp. <i>acuta</i>	17
<i>Desmodium grahami</i>	2	(<i>Gentiana strictiflora</i>)	
<i>Desmodium rosei</i>	1	<i>Geranium</i> spp.	16
<i>Disporum trachycarpum</i>	16	<i>Geranium caespitosum</i>	133
<i>Draba</i> spp.	3	(<i>G. fremontii</i>)	
<i>Draba asprella</i>	2	<i>Geranium lentum</i>	1
<i>Draba aurea</i>	3	<i>Geranium richardsonii</i>	149
<i>Draba helleriana</i>	47	<i>Geum aleppicum</i> ssp. <i>strictum</i>	4
		(<i>G. strictum</i>)	
		<i>Gnaphalium</i> spp.	25

<i>Gnaphalium macounii</i>	3	<i>Linathus nuttallii</i>	6
(<i>G. viscosum</i>)		(<i>Linanthastrum nuttallii</i>)	
<i>Goodyera oblongifolia</i>	67	<i>Linum</i> spp. (annuals)	15
<i>Goodyera repens</i>	14	<i>Linum aristatum</i>	1
<i>Grindelia</i> spp.	1	<i>Linum lewisii</i>	19
<i>Gutierrezia wrightii</i>	1	<i>Linum neomexicanum</i>	2
(<i>Xanthocephalum wrightii</i>)		<i>Lithospermum cobrense</i>	5
<i>Habenaria</i> spp.	10	<i>Lithospermum multiflorum</i>	153
(<i>Limnorchis</i> spp.)		<i>Lobelia anatina</i>	2
<i>Habenaria hyperborea</i>	1	<i>Lotus</i> spp.	2
(<i>Limnorchis hyperborea</i>)		<i>Lotus wrightii</i>	61
<i>Hackelia ursina</i>	6	<i>Lotus X nummularius</i>	2
<i>Halenia recurva</i>	12	(<i>L. wrightii X rigidus</i> , <i>Hosackia rigida</i>)	
<i>Haplopappus parryi</i>	162	<i>Lupinus</i> spp.	15
(<i>Oreochrysum parryi</i> , <i>Solidago parryi</i>)		<i>Lupinus kingii</i>	6
<i>Hedeoma</i> spp.	2	<i>Lupinus neomexicanus</i>	5
<i>Hedeoma hyssopifolium</i>	2	<i>Machaeranthera bigelovii</i>	4
<i>Hedeoma oblongifolium</i>	9	(<i>M. pattersonii</i> , <i>Aster bigelovii</i>)	
<i>Hedyotis pygmaea</i>	40	<i>Machaeranthera pinnatifida</i>	2
(<i>Houstonia wrightii</i>)		(<i>Haplopappus spinulosus</i>)	
<i>Helianthella parryi</i>	10	<i>Macromeria viridiflora</i>	7
<i>Helianthella quinquenervis</i>	14	<i>Malaxis ehrenbergii</i>	7
<i>Helianthus</i> spp.	1	<i>Malaxis soulei</i>	14
<i>Heterotheca fulcrata</i>	15	(<i>M. macrostachya</i>)	
(<i>H. villosa</i> , <i>Chrysopsis fulcrata</i> , <i>C. villosa</i> var. <i>foliosa</i> .)		<i>Mammillaria</i> spp.	3
<i>Heuchera</i> spp.	21	(Some species synonymous with some <i>Coryphantha</i> spp.)	
<i>Heuchera novomexicana</i>	2	<i>Mertensia franciscana</i>	35
<i>Hieracium fendleri</i>	88	<i>Mimulus guttatus</i>	3
<i>Hieracium rusbyi</i>	4	<i>Monarda austromontana</i>	1
<i>Hydrophyllum fendleri</i>	1	<i>Monarda menthaefolia</i>	15
(<i>H. occidentale</i>)		(<i>M. fistulosa</i> var. <i>menthaefolia</i>)	
<i>Hymenopappus filifolius</i>	1	<i>Monardella odoratissima</i>	1
(<i>H. lugens</i>)		<i>Moneses uniflora</i>	6
<i>Hymenopappus mexicanus</i>	18	(<i>Pyrola uniflora</i>)	
<i>Hymenopappus radiatus</i>	15	<i>Monotropa latisquama</i>	11
<i>Hymenoxys richardsonii</i>	14	(<i>M. hypopitys</i> var. <i>latisquama</i>)	
<i>Hypericum formosum</i>	3	<i>Oenothera</i> spp.	4
<i>Ipomoea</i> spp.	6	<i>Oenothera hookeri</i>	3
<i>Ipomoea costellata</i>	3	<i>Oenothera laciniata</i>	9
<i>Ipomopsis aggregata</i>	82	(<i>O. pubescens</i>)	
(<i>Gilia aggregata</i>)		<i>Opuntia</i> spp. (prickly pears)	12
<i>Iris missouriensis</i>	26	<i>Opuntia phaeacantha</i>	1
<i>Kuhnia chlorolepis</i>	12	(<i>O. engelmannii</i>)	
(<i>K. rosmarinifolia</i> , <i>Brickellia</i> <i>chlorolepis</i>)		<i>Opuntia spinosior</i>	1
<i>Lactuca graminifolia</i>	2	<i>Orthocarpus luteus</i>	1
<i>Lappula redowskii</i>	2	<i>Orthocarpus purpureo-albus</i>	1
<i>Lathyrus</i> spp.	4	<i>Osmorhiza depauperata</i>	57
<i>Lathyrus arizonicus</i>	170	(<i>O. obtusa</i>)	
<i>Lathyrus graminifolius</i>	46	<i>Oxalis metcalfei</i>	53
<i>Lathyrus leucanthus</i>	4	(<i>O. alpina</i>)	
(<i>L. lanzwertii</i>)		<i>Oxybaphus comatus</i>	3
<i>Lepidium densiflorum</i>	3	(<i>Mirabelis oblongifolia</i>)	
<i>Lepidium virginicum</i>	1	<i>Oxybaphus linearis</i>	12
(<i>L. medium</i>)		(<i>Mirabelis linearis</i>)	
<i>Leucelene ericoides</i>	5	<i>Oxypolis fendleri</i>	3
(<i>Aster arenosus</i> , <i>A. hirtifolius</i>)		<i>Oxytropis lambertii</i>	19
<i>Ligusticum porteri</i>	36	<i>Pedicularis</i> spp.	2
<i>Limnorchis hyperborea</i>	1	<i>Pedicularis angustifolia</i>	12
(<i>Habenaria hyperborea</i>)		(<i>P. angustissima</i>)	
		<i>Pedicularis centranthera</i>	4

<i>Pedicularis grayi</i>	25	<i>Senecio bigelovii</i>	33
<i>Pedicularis racemosa</i>	3	(<i>Ligularia bigelovii</i>)	
<i>Penstemon</i> spp.	21	<i>Senecio cardamine</i>	40
<i>Penstemon barbatus</i>	123	<i>Senecio cynthioides</i>	25
<i>Penstemon deaveri</i>	4	<i>Senecio douglasii</i>	1
(<i>P. virgatus</i> ssp. <i>arizonicus</i>)		<i>Senecio eremophilus</i>	11
<i>Penstemon linarioides</i>	2	<i>Senecio neomexicanus</i>	145
<i>Penstemon oliganthus</i>	10	<i>Senecio quaerens</i>	9
(<i>P. griffinii</i>)		<i>Senecio wootonii</i>	137
<i>Penstemon pinifolius</i>	12	<i>Sidalcea neomexicana</i>	2
<i>Penstemon virgatus</i>	2	<i>Silene laciniata</i>	17
(<i>P. putus</i>)		<i>Silene scouleri</i>	30
<i>Penstemon whippleanus</i>	3	<i>Sisymbrium</i> spp.	3
<i>Pericome caudata</i>	2	(Some species synonymous with	
<i>Petalostemon candidum</i>	11	<i>Thelypodopsis</i> spp.)	
(<i>Dalea candida</i> var. <i>oligophylla</i> , <i>Dalea oligophylla</i>)		<i>Sisymbrium altissimum</i>	5
<i>Phacelia</i> spp.	15	<i>Sisymbrium linearifolium</i>	45
<i>Phaseolus</i> spp.	1	(<i>Thelypodopsis linearifolia</i>)	
<i>Phaseolus metcalfei</i>	9	<i>Sisyrinchium arizonicum</i>	1
<i>Plantago major</i>	1	<i>Sisyrinchium demissum</i>	1
<i>Plantago patagonica</i>	3	(<i>S. angustifolium</i>)	
(<i>P. purshii</i>)		<i>Smilacina racemosa</i>	102
<i>Polemonium</i> spp.	6	<i>Smilacina stellata</i>	116
<i>Polygonum sawatchensis</i>	4	<i>Solanum</i> spp.	1
<i>Potentilla</i> spp.	20	<i>Solidago</i> spp.	59
<i>Potentilla concinna</i>	1	<i>Solidago missouriensis</i>	1
<i>Potentilla crinita</i>	11	<i>Solidago sparsiflora</i>	3
<i>Potentilla gracilis</i> var. <i>pulcherrima</i>	22	<i>Solidago spathulata</i> var. <i>neomexicana</i>	3
<i>Potentilla hippiana</i>	22	(<i>S. decumbens</i>)	
<i>Potentilla pennsylvanica</i>	3	<i>Solidago wrightii</i>	7
<i>Potentilla thurberi</i>	18	<i>Sonchus asper</i>	1
<i>Primula ellisiae</i>	8	<i>Sphaeralcea coccinea</i>	17
<i>Prunella vulgaris</i>	12	<i>Spiranthes parasitica</i>	2
<i>Pseudocymopterus montanus</i>	205	<i>Stachys coccinea</i>	3
<i>Pseudostellaria jamesiana</i>	2	<i>Stellaria</i> spp.	7
(<i>Stellaria jamesiana</i>)		<i>Stellaria longifolia</i>	3
<i>Psoralea tenuiflora</i>	3	<i>Stellaria longipes</i>	1
<i>Pteridium aquilinum</i>	108	(<i>S. laeta</i>)	
<i>Pterospora andromeda</i>	10	<i>Stephanomeria exigua</i>	1
<i>Pyrola chlorantha</i>	65	<i>Stevia</i> spp.	11
(<i>P. virens</i>)		<i>Stevia plummerae</i>	1
<i>Pyrola picta</i>	24	<i>Stevia serrata</i>	1
<i>Ramischia secunda</i>	74	<i>Streptopus amplexifolius</i>	1
(<i>Pyrola secunda</i> , <i>Orthilia secunda</i>)		<i>Swertia radiata</i>	43
<i>Ranunculus</i> spp.	3	(<i>Frasera speciosa</i>)	
<i>Ranunculus hydrocharoides</i>	1	<i>Taraxacum</i> spp.	19
<i>Ranunculus inamoenus</i>	1	<i>Thalictrum fendleri</i>	167
<i>Ratibida columnaris</i>	2	<i>Thermopsis pinetorum</i>	49
<i>Rudbeckia laciniata</i>	4	(<i>T. divaricarpa</i> , <i>T. rhombifolia</i>)	
<i>Rumex acetosella</i>	4	<i>Thlaspi montanum</i> var. <i>montanum</i>	58
(<i>Acetosella vulgaris</i>)		(<i>T. alpestre</i> , <i>T. fendleri</i>)	
<i>Rumex crispus</i>	2	<i>Townsendia formosa</i>	31
<i>Rumex occidentalis</i>	3	<i>Tradescantia pinetorum</i>	11
<i>Salvia davidsonii</i>	1	<i>Tragia stylaris</i>	11
<i>Saxifraga</i> spp.	2	(<i>T. ramosa</i>)	
<i>Scrophularia parviflora</i>	2	<i>Tragopogon</i> spp.	6
<i>Sedum</i> spp.	19	<i>Trifolium</i> spp.	6
<i>Senecio</i> spp.	10	<i>Trifolium longipes</i>	1
(<i>Packera</i> spp.)		(<i>T. neurophyllum</i>)	
<i>Senecio actinella</i>	12	<i>Urtica</i> spp.	1
		<i>Valeriana</i> spp.	2

<i>Valeriana capitata</i>	41
(<i>V. capitata</i> ssp. <i>acutiloba</i> , <i>V. arizonica</i>)	
<i>Valeriana edulis</i>	10
<i>Veratrum californicum</i>	2
<i>Verbascum thapsus</i>	9
<i>Verbena</i> spp.	2
<i>Verbena macdougalii</i>	2
<i>Veronica</i> spp.	1
<i>Veronica americana</i>	1
<i>Veronica peregrina</i>	1
<i>Veronica serpyllifolia</i>	1
<i>Vicia</i> spp.	4
<i>Vicia americana</i>	144
<i>Vicia leucophaea</i>	11
<i>Vicia pulchella</i>	57
<i>Viguiera</i> spp.	2
<i>Viguiera cordifolia</i>	7
<i>Viguiera multiflora</i>	33
(<i>Heliomeris multiflora</i>)	

<i>Viola canadensis</i>	154
<i>Viola nephrophylla</i>	6
<i>Woodsia</i> spp.	7
(<i>W. plummerae</i>)	
<i>Zygadenus</i> spp.	9
<i>Zygadenus elegans</i>	37
(<i>Anticlea elegans</i>)	
<i>Zygadenus virescens</i>	5

¹Because sampling was not statistically proportional, the frequency of a given species cannot be obtained in the usual manner whereby occurrences (number of plots in which a species is found) is divided by the total number of plots sampled. A zero value indicates presence in the stand, but outside the sample plot.

²These two are distinct species, but the two names both have been misapplied to the other species (S.C.S. 1982a 1982b).

³The preferred name for most varieties of this species is *Aster falcatus*, but our herbarium specimens were identified only as "*A. commutatus*" and varietal correspondence was not possible.

**Appendix C. Successional Status of Major Tree Species
Within Habitat Types on the Apache, Gila, and
Cibola (Magdalena District) National Forests¹**

	PIEN	ABLA	ABCO	PIPU	PSME	PIST	POTR	PIPO	PIED	JUDE	JUMO	JUSC	QUGA	QUGR	ACNE	ALOB	JUMA	PO
1. PIEN/Moss	C		a		S	S	s											
2. PIEN/VAMY	C		a		S	S	S											
3. PIEN/SECA																		
ABLA phase	C	C	s	s	S	s	S											
ABCO phase	C	c	S	s	S	s	S	a										
4. PIEN/EREX	C	a	c	s	C	s	S	s										
5. ABLA/VAMY																		
VAMY (typic) phase	C	C			s	s	s											
RUPA phase	C	C	s	a	S	s	S											
6. ABLA/LAAR	C	C			S	S	S											
7. ABLA/HODU (Scree)	c	C			C	C	s											
8. ABLA/EREX	C	C	s	s	S	s	S											
9. ABLA/RUPA	C	C	S		S	s	S											
10. PIPU/SECA	c	c	S	C	S	S	s											
11. PIPU/EREX	c	a	c	C	C	S	S	s										
12. PIPU/CAFO	c	a		C	C	S	S	S										
13. PIPU/FEAR	a	a	c	C	C	s	s	S										
14. PIPU/POPR	c			C	C	s	s											
15. ABCO/EREX	a	a	C	a	C	S	S	s										
16. ABCO/Sparse	a	a	C		C	S	s	s										
17. ABCO/HODU (Scree)			C		C	S	S	S										
18. ABCO/ACGL	a	a	C	a	C	S	S	s										
19. ABCO/MUVI			C	a	C	S	s	S					s					
20. ABCO/QUGA																		
QUGA (typic) phase			C	a	C	S		S					S					
MUVI phase			C		C	S		S					S					
21. ABCO/RONE	a		C		C	S	S	S										
22. ABCO/FEAR																		
FEAR (typic) phase			C		C	s	s	s										
POFE phase			C	a	C	s	s	s										
23. ABCO/ACGR			C		c		s	s								c		
24. ABCO/JUMA			C		c			S					C		c		C	
25. PSME/ARUV					C	C	S	S										
26. PSME/HODU (Scree)					C	C	s											
27. PSME/FEAR			a		C	S	s	S	a									
28. PSME/BRCI			a		C	S	S	a										
29. PSME/QUGA																		
QUGA (typic) phase			a		C	s		S	s	s		s	S					
MUVI phase			a		C	s		c		a			S					
FEAR phase			a		C	s		C	s				S					
30. PSME/MUVI			a	a	C	S	s	S	a	s								
31. PSME/MUMO			a		C	s		S	s	s		s						
32. PSME/QUHY			a		C	s		C	s				s					
33. PIPO/MUVI																		
MUVI (typic) phase					a	c		C	a	a								
QUGA phase			a		c	c		C	s	s			S					
34. PIPO/MUVI-FEAR																		
MUVI-FEAR (typic) phase					a	a		C	a	s								
QUGA phase								C	a				S					
BOGR phase								C	s	s								
35. PIPO/QUGR																		
MUMO phase					c	a		C	c	c	a					C		
MULO phase					a			C	C	C						C		
36. PIPO/Rockland					c	a		C	c	c						c		
37. PIPO/FEAR																		
FEAR (typic) phase								C	a	a								
QUGA phase								C	a	s			S					
BOGR phase								C	s	s								
38. PIPO/MUMO					a			C	S	S	a		s	s				
39. PIPO/QUGA																		
QUGA (typic) phase					a			C	s	s			S					
MULO phase					a			C	s	s			S					
40. PIPO/BOGR																		
PIED phase								C	C	C	s		s	s				
VIAR phase								C		C							S	
41. PIPO/ARPU CT								C	s	C			S					
42. POAN Series			c		c			s	a	s		c	S		c	c	c	c

¹Successional status interpreted from sample data, and some variation can be expected. An upper case letter indicates that a species was found on most plots in the habitat type. A lower case letter indicates that a species was found infrequently. Climax status is indicated by either C or c, and seral status by S or s.

Appendix D. Average density and constancy of major tree species and average cover and constancy of major herbaceous species within each habitat type on the Apache, Gila, and Cibola (Magdalena District) National Forests

Table 1.--Tree density (D) or shrub-herb cover (C) and constancy (CON) for Apache-Gila-Cibola(Madg.): Picea engelmannii series.

HTs:	PIEN/Moss		PIEN/VAMY		PIEN/SECA ABLA ph. (8)		PIEN/SECA ABCO ph. (12)		PIEN/EREX (7)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
No. plots:	(3)		(3)		(8)		(12)		(7)	
Trees										
Abies concolor - Young regen.			3	33	4	63	23	100	15	57
Abies concolor - Advance regen.	<1	33	1	33	1	38	3	58	1	57
Abies concolor - Mature							<1	25	<1	29
Abies lasiocarpa - Young regen.					28	100	1	42	<1	14
Abies lasiocarpa - Advance regen.					4	88			<1	14
Abies lasiocarpa - Mature					3	100	<1	8		
Alnus oblongifolia - Young regen.										
Alnus oblongifolia - Advance regen.										
Alnus oblongifolia - Mature										
Juniperus deppeana - Young regen.										
Juniperus deppeana - Advance regen.										
Juniperus deppeana - Mature										
Juniperus osteosperma - Young regen.										
Juniperus osteosperma - Advance regen.										
Juniperus osteosperma - Mature										
Juniperus scopulorum - Young regen.										
Juniperus scopulorum - Advance regen.										
Juniperus scopulorum - Mature										
Picea engelmannii - Young regen.	22	100	45	100	10	100	23	100	32	100
Picea engelmannii - Advance regen.	18	100	23	100	6	88	9	100	13	100
Picea engelmannii - Mature	5	67	6	100	3	88	3	100	4	86
Picea pungens - Young regen.					1	38	2	67	6	43
Picea pungens - Advance regen.					<1	38	1	42	5	57
Picea pungens - Mature					<1	25	<1	33	<1	14
Pinus edulis - Young regen.										
Pinus edulis - Advance regen.										
Pinus edulis - Mature										
Pinus ponderosa - Young regen.					<1	13	<1	8		
Pinus ponderosa - Advance regen.					<1	13	<1	17	<1	29
Pinus ponderosa - Mature										
Pinus strobiformis - Young regen.	13	100	10	100	1	38	2	50	2	43
Pinus strobiformis - Advance regen.	6	67	1	67	1	50	2	50	<1	29
Pinus strobiformis - Mature	1	67	<1	33			<1	42		

(Continued)

Table 1.--(continued).

HTs:	PIEN/Moss		PIEN/VAMY		PIEN/SECA ABLA ph.		PIEN/SECA ABCO ph.		PIEN/EREX	
No. plots:	(3)		(3)		(8)		(12)		(7)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
Populus angustifolia - Young regen.										
Populus angustifolia - Advance regen.										
Populus angustifolia - Mature										
Populus tremuloides - Young regen.										
Populus tremuloides - Advance regen.	2	100	2	33					3	43
Populus tremuloides - Mature	<1	67	5	67	2	50	1	50	1	71
Pseudotsuga menziesii - Young regen.	4	67	21	100	9	100	10	100	13	100
Pseudotsuga menziesii - Advance regen.	11	67	1	67	2	75	3	83	4	86
Pseudotsuga menziesii - Mature	5	67	3	67	4	100	3	92	3	86
Shrubs										
Acer glabrum	2	33	<1	67			<1	25		
Acer grandidentatum										
Acer negundo										
Alnus oblongifolia										
Berberis repens										
Calliandra humilis										
Ceanothus fendleri										
Cercocarpus montanus										
Chimaphila umbellata								8		
Cornus stolonifera								8		
Fraxinus pennsylvanica										
Garrya wrightii										
Gutierrezia sarothrae										
Holodiscus dumosus										
Hymenoxys richardsonii	<1	33								
Jamesia americana			<1	100						
Juglans major										
Juniperus communis	2	67	2	33						
Lonicera albiflora										
Lonicera arizonica										
Nolina microcarpa	<1	67	<1	33						
Parthenocissus vitacea										
Philadelphus spp.										
Physocarpus monogynus	<1	67	<1	33						

(Continued)

Table 1.—(continued).

HTs:	PIEN/Moss		PIEN/VAMY		PIEN/SECA ABLA ph. (8)		PIEN/SECA ABCO ph. (12)		PIEN/EREX	
No. plots:	(3)		(3)		(8)		(12)		(7)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
Populus tremuloides - shrubs	<1	67	<1	33	<1	75	<1	67	<1	86
Ptelea trifoliata										
Prunus emarginata										
Prunus virginiana									<1	14
Quercus chrysolepis										
Quercus emoryi										
Quercus gambelii										
Quercus grisea										
Quercus hypoleucoides										
Quercus rugosa										
Rhamnus betulaeifolia										
Rhus glabra										
Rhus trilobata										
Ribes cereum										
Ribes montigenum										
Ribes pinetorum	<1	33	<1	33			<1	17		
Ribes wolfii	<1	33	<1	33						
Robinia neomexicana					<1	38				
Rosa spp.										
Rubus arizonensis										
Rubus parviflorus										
Rubus strigosus					<1	63	<1	67	<1	43
Salix bebbiana					<1	13	<1	17		
Salix scouleriana										
Salix spp.			1	33	<1	25			2	57
Sambucus spp.										
Shepherdia canadensis										
Sorbus dumosa					<1	13				
Symphoricarpus oreophilus										
Toxicodendron rydbergii										
Vaccinium myrtillus										
Vitis arizonica	<1	33		14			<1	8		
Yucca baccata										
Yucca schottii										

(Continued)

Table 1.--(continued).

HTs:	PIEN/Moss	PIEN/VAMY	PIEN/SECA ABLA ph. (8)	PIEN/SECA ABCO ph. (12)	PIEN/EREX
No. plots:	(3) D/C CON	(3) D/C CON	(8) D/C CON	(12) D/C CON	(7) D/C CON
Graminoids					
Agropyron arizonicum					
Agropyron (smithii?)					
Agrostis alba					
Andropogon spp.					
Andropogon cirratus					
Andropogon gerardi					
Andropogon scoparius					
Aristida spp.					
Aristida arizonica					
Aristida fendleriana					
Blepharoneuron tricholepis					
Bouteloua curtipendula					
Bouteloua gracilis					
Bromus anomalus					
Bromus carinatus					
Bromus ciliatus	<1	67	<1	100	<1 14
Bromus frondosus				4	100
Bromus lanatipes					
Bromus spp.					
Calamagrostis canadensis					
Carex spp.	<1	33	<1	67	<1 43
Carex foenea			1	63	10 71
Carex lanuginosa				1	75
Carex microptera					
Carex occidentalis					
Carex rossii			<1	75	<1 14
Cyperus rusbyi				<1	83
Cyperus sp.					
Elymus glaucus					
Festuca arizonica					
Festuca sororia			<1	38	3 29
Glyceria elata			<1	<1	<1 43
Glyceria striata					

(Continued)

Table 1.--(continued).

HTs:	PIEN/Moss (3)	PIEN/VAMY		PIEN/SECA ABLA ph. (8)		PIEN/SECA ABCO ph. (12)		PIEN/EREX (7)	
		D/C	CON	D/C	CON	D/C	CON	D/C	CON
No. plots:	(3)								
Koeleria nitida		<1		<1	13	<1	50	<1	14
Luzula parviflora									
Lycurus phleoides						<1	8		
Melica porteri									
Muhlenbergia longiligula									
Muhlenbergia montana						<1		<1	14
Muhlenbergia monticola									
Muhlenbergia pauciflora									
Muhlenbergia rigens									
Muhlenbergia virescens						<1	8	1	14
Muhlenbergia wrightii									
Panicum bulbosum									
Piptochaetium fimbriatum									
Poa compressa				<1	13	<1	42	<1	29
Poa fendleriana									
Poa nervosa var tracyi				<1		<1	17	1	29
Poa pratensis				<1		<1	25	<1	14
Sitanion hystrix									
Sporobolus cryptandrus									
Stipa spp.									
Stipa pringlei									
Trisetum montanum		<1	33	<1	38	<1	25	<1	29
Forbs									
Achillea millefolium									
Actaea rubra ssp. arguta									
Agrimonia striata									
Allium cernuum						<1	25	<1	43
Allium kunthii						<1	17		
Allium rhizomatum									
Antennaria marginata									
Antennaria parvifolia									
Antennaria spp.		<1	33						
Aquilegia chrysantha						<1	8		

(Continued)

HTs:	PIEN/Moss	PIEN/VAMY	PIEN/SECA	PIEN/SECA	PIEN/EREX
No. plots:	(3)	(3)	ABLA ph. (8)	ABCO ph. (12)	(7)
	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
<i>Aquilegia elegantula</i>			<1	38	<1
<i>Aquilegia triternata</i>			<1	13	<1
<i>Arabis</i> spp.					
<i>Arenaria lanuginosa</i>			<1	13	<1
<i>Arenaria</i> spp.	<1	33			<1
<i>Artemisia carruthii</i>					
<i>Artemisia dracunculoides</i>					
<i>Artemisia franserioides</i>			<1	25	<1
<i>Artemisia frigida</i>					
<i>Artemisia ludoviciana</i>					
<i>Asclepias</i> spp.					
<i>Aster falcatus</i>					
<i>Astragalus egglestonii</i>					
<i>Astragalus gilensis</i>					
<i>Astragalus humistratus</i>					
<i>Astragalus</i> spp.					
<i>Bahia dissecta</i>					
<i>Brickellia brachyphylla</i>					
<i>Brickellia fendleri</i>					
<i>Brickellia grandiflora</i>					
<i>Brickellia</i> spp.					
<i>Calypso bulbosa</i>					
<i>Campanula rotundifolia</i>			<1	13	<1
<i>Cardamine cordifolia</i>					
<i>Castilleja</i> spp.					
<i>Chaptalia alsophila</i>					<1
<i>Chamerion angustifolium</i>					<1
<i>Cicuta douglasii</i>			<1	25	<1
<i>Circaea alpina</i>					
<i>Cirsium</i> spp.			<1	13	<1
<i>Cirsium parryi</i>					
<i>Cirsium wheeleri</i>					
<i>Clematis ligusticifolia</i>					
<i>Clematis pseudoalpina</i>	<1	67	<1	13	<1

(Continued)

Table 1.--(continued).

HTs:	PIEN/Moss		PIEN/VAMY		PIEN/SECA ABLA ph.		PIEN/SECA ABCO ph.		PIEN/EREX	
No. plots:	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
(3)										
<i>Cologania longifolia</i>										
<i>Commelina dianthifolia</i>										
<i>Corallorhiza</i> spp.										
<i>Corallorhiza maculata</i>										
<i>Cryptantha jamesii</i>										
<i>Cucurbita foetidissima</i>										
<i>Cystopteris fragilis</i>										
<i>Delphinium tenuisectum</i>										
<i>Desmanthus cooleyi</i>										
<i>Disporum trachycarpum</i>										
<i>Draba helleriana</i>										
<i>Dugaldia hoopesii</i>										
<i>Equisetum arvense</i>										
<i>Equisetum laevigatum</i>										
<i>Erigeron concinnus</i>										
<i>Erigeron delphinifolius</i>										
<i>Erigeron divergens</i>										
<i>Erigeron eximius</i>										
<i>Erigeron flagellaris</i>										
<i>Erigeron formosissimus</i>										
<i>Erigeron platyphyllus</i>										
<i>Eriogonum alatum</i>										
<i>Eriogonum jamesii</i>										
<i>Erysimum capitatum</i>										
<i>Fragaria americana</i>										
<i>Fragaria ovalis</i>										
<i>Galium</i> spp.										
<i>Galium fendleri</i>										
<i>Galium mexicanum</i>										
<i>Gaura hexandra</i>										
<i>Gentianella amarella</i> s. <i>acuta</i>										
<i>Geranium caespitosum</i>										
<i>Geranium richardsonii</i>										
<i>Geranium</i> spp.										

(Continued)

Table 1.--(continued).

HTs:	PIEN/Moss	PIEN/VAMY	PIEN/SECA	PIEN/SECA	PIEN/EREX
No. plots:	(3)	(3)	ABLA ph.	ABCO ph.	(7)
	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
<i>Geum aleppicum</i> ssp. <i>strictum</i>					
<i>Gnaphalium macounii</i>			<1	<1	<1
<i>Goodyera oblongifolia</i>		100	50	50	29
<i>Goodyera repens</i>		<1	<1	17	17
<i>Halenia recurva</i>		<1	38	17	17
<i>Haplopappus parryi</i>	<1	<1	<1	17	71
<i>Hedeoma oblongifolium</i>					
<i>Hedyotis pygmaea</i>					
<i>Helianthella parryi</i>					
<i>Heterotheca fulcrata</i>					
<i>Hieracium fendleri</i>					<1
<i>Hydrophyllum fendleri</i>					14
<i>Hymenopappus filifolius</i>					
<i>Hymenopappus mexicanus</i>					
<i>Hypericum formosum</i>					
<i>Ipomopsis aggregata</i>				<1	17
<i>Iris missouriensis</i>					
<i>Kuhnia chlorolepis</i>					
<i>Lactuca graminifolia</i>					
<i>Lathyrus arizonicus</i>			<1	3	6
<i>Lathyrus graminifolius</i>			50	92	100
<i>Leucelene ericoides</i>					
<i>Ligusticum porteri</i>			<1	<1	<1
<i>Linum lewisii</i>	<1	33	25	17	43
<i>Lithospermum multiflorum</i>			<1	<1	<1
<i>Lobelia anatina</i>			13	17	14
<i>Lotus wrightii</i>					
<i>Lupinus neomexicanus</i>					
<i>Lupinus</i> spp.					
<i>Malaxis ehrenbergii</i>					
<i>Malaxis soulei</i>					
<i>Mertensia franciscana</i>			<1	<1	<1
<i>Monarda menthaefolia</i>			13	42	14
<i>Opuntia</i> spp. (prickly pears)					

(Continued)

Table 1.—(continued).

HTs:	PIEN/Moss	PIEN/VAMY	PIEN/SECA	PIEN/SECA	PIEN/EREX			
No. plots:	(3)	(3)	ABLA ph.	ABCO ph.	(7)			
	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON			
Osmorhiza depauperata			<1	63	<1	50	<1	29
Oxalis metcalfei			<1	13	<1	8	<1	14
Oxybaphus linearis								
Oxypolis fendleri								
Oxytropis lambertii								
Pedicularis angustifolia								
Pedicularis grayii							<1	14
Pedicularis racemosa								
Penstemon barbatus								
Penstemon linarioides								
Penstemon oliganthus								
Penstemon pinifolius								
Penstemon whippleanus								
Petalostemon candidum							<1	14
Polygonum sawatchensis								
Potentilla crinita								
Potentilla gracilis v pulcher							<1	14
Potentilla hippiana								
Potentilla spp.								
Potentilla thurberi						8	<1	
Prunella vulgaris			<1	25	<1	8	<1	
Pseudocymopterus montanus	<1	33	<1	13	<1	50	<1	86
Pseudostellaria jamesiana								
Psoralea tenuiflora								
Pteridium aquilinum			4	75	1	83	<1	43
Pterospora andromeda								
Pyrola chlorantha	<1	67	<1	63	<1	67	<1	43
Pyrola picta						8	<1	
Ramischia secunda	<1	33	<1	88	<1	75	<1	43
Ratibida columnaris								
Rudbeckia laciniata								
Rumex acetosella								
Rumex crispus								
Rumex occidentalis								
Senecio actinella								

(Continued)

Table 1.--(continued).

HTs:	PIEN/Moss		PIEN/VAMY		PIEN/SECA ABLA ph.		PIEN/SECA ABCO ph.		PIEN/EREX	
No. plots:	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
(3)	(3)	(3)	(8)	(12)	(7)					
<i>Senecio bigelovii</i>			<1	13	<1	8	<1	14		
<i>Senecio cardamine</i>			17	88	11	100				
<i>Senecio cynthioides</i>										
<i>Senecio eremophilus</i>										
<i>Senecio neomexicanus</i>										
<i>Senecio quaerens</i>										
<i>Senecio wootoni</i>			1	75	<1	67	<1	43		
<i>Sidalcea neomexicana</i>										
<i>Silene laciniata</i>										
<i>Silene scouleri</i>					<1	8				
<i>Sisymbrium linearifolium</i>										
<i>Smilacina racemosa</i>	<1	33	<1	67	<1	25	<1	14		
<i>Smilacina stellata</i>	<1	33	<1	38	<1	50	1	57		
<i>Solidago spathulata</i> var <i>neomex</i>										
<i>Solidago</i> spp.			<1	25	<1	25				
<i>Solidago wrightii</i>										
<i>Sphaeralcea coccinea</i>										
<i>Swertia radiata</i>			<1	13	<1	17	<1	14		
<i>Taraxacum</i> spp.										
<i>Thalictrum fendleri</i>			<1	63	<1	58	2	86		
<i>Thermopsis pinetorum</i>			<1	13	5	25	2	14		
<i>Townsendia formosa</i>					<1	17	<1	14		
<i>Tragia stylaris</i>										
<i>Valeriana capitata</i>					<1	8	3	14		
<i>Valeriana edulis</i>										
<i>Veratrum californicum</i>										
<i>Verbascum thapsus</i>										
<i>Vicia americana</i>			<1	38	<1	50	1	86		
<i>Vicia leucophaea</i>										
<i>Vicia pulchella</i>										
<i>Viguiera multiflora</i>										
<i>Viola canadensis</i>	<1	33	<1	67	2	100	2	86		
<i>Viola nephrophylla</i>										
<i>Zygadenus elegans</i>	<1	67	<1	67	<1		<1	29		
<i>Zygadenus virescens</i>										

Table 2.—Tree density (D) or shrub-herb cover (C) and constancy (CON) for Apache-Gila-Cibola(Madg.): *Abies lasiocarpa* series.

HTs:	ABLA/VAMY Typic ph. (13)	ABLA/VAMY RUPA ph. (6)	ABLA/LAAR D/C CON	ABLA/HODU D/C CON	ABLA/EREX D/C CON	ABLA/RUPA D/C CON
No. plots:	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
Trees						
<i>Abies concolor</i> - Young regen.		5	67		3	16
<i>Abies concolor</i> - Advance regen.		<1	33		<1	12
<i>Abies concolor</i> - Mature		<1	17		<1	8
<i>Abies lasiocarpa</i> - Young regen.	<1	8				
<i>Abies lasiocarpa</i> - Advance regen.	44	100	100	4	100	14
<i>Abies lasiocarpa</i> - Mature	12	100	100	1	100	1
<i>Abies lasiocarpa</i> - Mature	2	85	83	2	100	2
<i>Alnus oblongifolia</i> - Young regen.						
<i>Alnus oblongifolia</i> - Advance regen.						
<i>Alnus oblongifolia</i> - Mature						
<i>Juniperus deppeana</i> - Young regen.						
<i>Juniperus deppeana</i> - Advance regen.						
<i>Juniperus deppeana</i> - Mature						
<i>Juniperus osteosperma</i> - Young regen.						
<i>Juniperus osteosperma</i> - Advance regen.						
<i>Juniperus osteosperma</i> - Mature						
<i>Juniperus scopulorum</i> - Young regen.						
<i>Juniperus scopulorum</i> - Advance regen.						
<i>Juniperus scopulorum</i> - Mature						
<i>Picea engelmannii</i> - Young regen.	37	100	100	1	100	1
<i>Picea engelmannii</i> - Advance regen.	29	100	83	1	100	
<i>Picea engelmannii</i> - Mature	7	100	83			
<i>Picea pungens</i> - Young regen.						
<i>Picea pungens</i> - Advance regen.						
<i>Picea pungens</i> - Mature						
<i>Pinus edulis</i> - Young regen.						
<i>Pinus edulis</i> - Advance regen.						
<i>Pinus edulis</i> - Mature						
<i>Pinus ponderosa</i> - Young regen.						
<i>Pinus ponderosa</i> - Advance regen.						
<i>Pinus ponderosa</i> - Mature						
<i>Pinus strobiformis</i> - Young regen.	<1	8	17	7	100	
<i>Pinus strobiformis</i> - Advance regen.	<1	15	50	5	100	
<i>Pinus strobiformis</i> - Mature	<1	8	17	7	100	

(Continued)

Table 2.-(continued).

HTs:	ABLA/VAMY Typic ph. (13)	ABLA/VAMY RUPA ph. (6)	ABLA/LAAR (1)	ABLA/HODU (1)	ABLA/EREX (25)	ABLA/RUPA (5)
No. plots:	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
Populus angustifolia - Young regen.	<1	8	2	50	3	100
Populus angustifolia - Advance regen.	<1	38	<1	50	3	100
Populus angustifolia - Mature	<1	15	7	67	5	100
Populus tremuloides - Young regen.	<1	23	4	67	1	100
Populus tremuloides - Advance regen.	<1	31	3	67	1	100
Populus tremuloides - Mature	<1	8	2	50	3	100
Pseudotsuga menziesii - Young regen.	<1	15	7	67	5	100
Pseudotsuga menziesii - Advance regen.	<1	23	4	67	1	100
Pseudotsuga menziesii - Mature	<1	31	3	67	1	100
Shrubs						
Acer glabrum	<1	15	6	67	4	100
Acer grandidentatum					<1	16
Acer negundo					16	11
Alnus oblongifolia						100
Berberis repens						
Calliandra humilis						
Ceanothus fendleri						
Cercocarpus montanus						
Chimaphila umbellata	<1	8	<1	17	<1	100
Cornus stolonifera			<1	17	<1	40
Fraxinus pennsylvanica						
Garrya wrightii						
Gutierrezia sarothrae						
Holodiscus dumosus						
Hymenoxys richardsonii	<1	8	<1	17	7	100
Jamesia americana					<1	8
Juglans major						<1
Juniperus communis	<1	15			3	100
Lonicera albiflora						36
Lonicera arizonica						
Nolina microcarpa						
Parthenocissus vitacea						
Philadelphus spp.						

(Continued)

Table 2.--(continued).

HTs:	ABLA/VAMY Typic ph. D/C	CON	ABLA/VAMY RUPA ph. (6) D/C	CON	ABLA/LAAR (1) D/C	CON	ABLA/HODU (1) D/C	CON	ABLA/EREX (25) D/C	CON	ABLA/RUPA (5) D/C	CON
No. plots:	(13)											
Physocarpus monogynus			3	67					<1	4	<1	40
Populus tremuloides - shrubs	<1	46	<1	83			<1	100	<1	72	<1	60
Ptelea trifoliata												
Prunus emarginata									<1	4		
Prunus virginiana												
Quercus chrysolepis												
Quercus emoryi												
Quercus gambelii												
Quercus grisea												
Quercus hypoleucoides												
Quercus rugosa												
Rhamnus betulaeifolia												
Rhus glabra												
Rhus trilobata												
Ribes cereum												
Ribes montigenum	<1	15										
Ribes pinetorum			<1	67	<1	100			<1	12	<1	60
Ribes wolfii	<1	46	<1	50			<1	100	<1	4	<1	40
Robinia neomexicana	<1	8	<1	50					<1	12	<1	60
Rosa spp.												
Rubus arizonensis												
Rubus parviflorus	<1	23	18	100	<1	100	<1	100	<1	52	8	100
Rubus strigosus	<1	8	<1	17					<1	8	2	40
Salix bebbiana												
Salix scouleriana	<1	23	5	33	4	100	<1	100	<1	16	<1	40
Salix spp.												
Sambucus spp.			<1	17	<1	100			<1	4	<1	20
Shepherdia canadensis									<1	8		
Sorbus dumosa			<1	50								
Symphoricarpus oreophilus	<1	46	<1	17	3	100			<1	8	<1	20
Toxicodendron rydbergii	<1	8	<1	17			13	100	<1	8	<1	20
Vaccinium myrtillus												
Vitis arizonica	38	100	33	100					<1	8		
Yucca baccata												
Yucca schottii												

(Continued)

Table 2.—(continued).

HTs:	ABLA/VAMY Typic ph. D/C	ABLA/VAMY RUPA ph. D/C	ABLA/LAAR D/C	ABLA/HODU D/C	ABLA/EREX D/C	ABLA/RUPA D/C
No. plots:	(13)	(6)	(1)	(1)	(25)	(5)
CON	CON	CON	CON	CON	CON	CON
Graminoids						
Agropyron arizonicum					<1	4
Agropyron (smithii?)						
Agrostis alba						
Andropogon spp.						
Andropogon cirratus						
Andropogon gerardi						
Andropogon scoparius						
Aristida spp.						
Aristida arizonica						
Aristida fendleriana						
Blepharoneuron tricholepis						
Bouteloua curtipendula						
Bouteloua gracilis						
Bromus anomalus						
Bromus carinatus						
Bromus ciliatus	<1	54	1	83	1	100
Bromus frondosus					2	<1
Bromus lanatipes						
Bromus spp.						
Calamagrostis canadensis						
Carex spp.						
Carex foenea	<1	33			<1	12
Carex lanuginosa					1	32
Carex microptera					<1	4
Carex occidentalis					<1	
Carex rossii					<1	52
Cyperus rusbyi	<1	31				
Cyperus sp.						
Elymus glaucus						
Festuca arizonica						
Festuca sororia	<1	15			<1	20
Glyceria elata					<1	4
Glyceria striata						

(Continued)

Table 2.--(continued).

HTs:	ABLA/VAMY Typic ph. (13)	ABLA/VAMY RUPA ph. (6)	ABLA/LAAR D/C CON	ABLA/HODU D/C CON	ABLA/EREX D/C CON	ABLA/RUPA D/C CON
No. plots:	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
Koeleria nitida	<1	8	<1	17	<1	12
Luzula parviflora						
Lycurus phleoides						
Melica porteri						
Muhlenbergia longiligula						
Muhlenbergia montana						
Muhlenbergia monticola						
Muhlenbergia pauciflora						
Muhlenbergia rigens						
Muhlenbergia virescens						
Muhlenbergia wrightii						
Panicum bulbosum						
Piptochaetium fimbriatum						
Poa compressa						
Poa fendleriana						
Poa nervosa var tracyi	<1	8	<1		<1	8
Poa pratensis					<1	4
Sitanion hystrix					<1	8
Sporobolus cryptandrus						
Stipa spp.						
Stipa pringlei						
Trisetum montanum	<1	31	<1	50	<1	48
Forbs						
Achillea millefolium						
Actaea rubra ssp. arguta						
Agrimonia striata						
Allium cernuum						
Allium kunthii						
Allium rhizomatum						
Antennaria marginata						
Antennaria parvifolia						
Antennaria spp.						
Aquilegia chrysantha						
Aquilegia elegantula	<1	15	<1		<1	20

(Continued)

Table 2.—(continued).

HTs:	ABLA/VAMY Typic ph. (13)		ABLA/VAMY RUPA ph. (6)		ABLA/LAAR (1)		ABLA/HODU (1)		ABLA/EREX (25)		ABLA/RUPA (5)	
No. plots:	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
Aquilegia triternata	<1	8									<1	40
Arabis spp.												
Arenaria lanuginosa	<1	8								<1	4	
Arenaria spp.										<1	8	
Artemisia carruthii												
Artemisia dracunculoides												
Artemisia franserioides	<1	15	1	67						<1	72	60
Artemisia frigida												
Artemisia ludoviciana												
Asclepias spp.												
Aster falcatus												
Astragalus egglestonii												
Astragalus gilensis												
Astragalus humistratus												
Astragalus spp.												
Bahia dissecta												
Brickellia brachyphylla												
Brickellia fendleri												
Brickellia grandiflora												
Brickellia spp.										<1	12	
Calypso bulbosa										<1	12	
Campanula rotundifolia												
Cardamine cordifolia												
Castilleja spp.							<1	100	<1	100	4	
Chaptalia alsophila												
Chamerion angustifolium												
Cicuta douglasii	<1	92	<1	67						<1	28	60
Circaea alpina												
Cirsium spp.											<1	4
Cirsium parryi											<1	4
Cirsium wheeleri											<1	20
Clematis ligusticifolia												
Clematis pseudoalpina	<1	8	<1	33						<1	4	80
Cologania longifolia												

(Continued)

Table 2.-(continued).

HTs:	ABLA/VAMY Typic ph. (13)		ABLA/VAMY RUPA ph. (6)		ABLA/LAAR (1)		ABLA/HODU (1)		ABLA/EREX (25)		ABLA/RUPA (5)	
No. plots:	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
<i>Commelina dianthifolia</i>												
<i>Corallorhiza</i> spp.									<1	4	<1	20
<i>Corallorhiza maculata</i>									<1	20	<1	20
<i>Cryptantha jamesii</i>					<1	100						
<i>Cucurbita foetidissima</i>												
<i>Cystopteris fragilis</i>											<1	20
<i>Delphinium tenuisectum</i>												
<i>Desmanthus cooley</i>												
<i>Disporum trachycarpum</i>											<1	80
<i>Draba helleriana</i>												
<i>Dugaldia hoopesii</i>	<1	8							<1	36		
<i>Equisetum arvense</i>												
<i>Equisetum laevigatum</i>												
<i>Erigeron concinnus</i>												
<i>Erigeron delphinifolius</i>												
<i>Erigeron divergens</i>												
<i>Erigeron eximius</i>	<1	62	2	83					14	96		
<i>Erigeron flagellaris</i>												
<i>Erigeron formosissimus</i>												
<i>Erigeron platyphyllus</i>												
<i>Eriogonum alatum</i>												
<i>Eriogonum jamesii</i>												
<i>Erysimum capitatum</i>												
<i>Fragaria americana</i>												
<i>Fragaria ovalis</i>	<1	46	<1	67	<1	100	<1	100	1	8	<1	20
<i>Galium</i> spp.			<1	17					2	80		
<i>Galium fendleri</i>												
<i>Galium mexicanum</i>												
<i>Gaura hexandra</i>												
<i>Gentianella amarella</i> s. <i>acuta</i>												
<i>Geranium caespitosum</i>												
<i>Geranium richardsonii</i>	<1	54	8	100	2	100	3	100	2	84	5	100
<i>Geranium</i> spp.												
<i>Geum aleppicum</i> ssp. <i>strictum</i>												

(Continued)

Table 2.—(continued).

HTs:	ABLA/VAMY Typic ph. (13)		ABLA/VAMY RUPA ph. (6)		ABLA/LAAR (1)		ABLA/HODU (1)		ABLA/EREX (25)		ABLA/RUPA (5)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
Gnaphalium macounii	<1	23	<1	50					<1	64	<1	80
Goodyera oblongifolia			<1	17					<1	4		
Goodyera repens												
Halenia recurva	1	100	2	67	2	100	3	100	2	80	<1	20
Haplopappus parryi												
Hedeoma oblongifolium												
Hedyotis pygmaea												
Helianthella parryi												
Heterotheca fulcrata												
Hieracium fendleri									<1	4		
Hydrophyllum fendleri												
Hymenopappus filifolius												
Hymenopappus mexicanus												
Hypericum formosum												
Ipomopsis aggregata												
Iris missouriensis												
Kuhnia chlorolepis												
Lactuca graminifolia												
Lathyrus arizonicus	<1	15	<1	17	20	100			4	72		
Lathyrus graminifolius												
Leucelena ericoides												
Ligusticum porteri	<1	23	<1	17	<1	100			<1	20	<1	40
Linum lewisii									<1	16		
Lithospermum multiflorum												
Lobelia anatina												
Lotus wrightii												
Lupinus neomexicanus												
Lupinus spp.									<1	4		
Malaxis ehrenbergii												
Malaxis soulei												
Mertensia franciscana	<1	15	<1	50					<1	28	3	20
Monarda menthaefolia												
Opuntia spp. (prickly pears)												
Osmorhiza depauperata	<1	15	<1	17					<1	40	<1	80

(Continued)

Table 2.-(continued).

HTs:	ABLA/VAMY Typic ph. (13)		ABLA/VAMY RUPA ph. (6)		ABLA/LAAR (1)		ABLA/HODU (1)		ABLA/EREX (25)		ABLA/RUPA (5)	
No. plots:	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
<i>Oxalis metcalfei</i>			<1	100								
<i>Oxybaphus linearis</i>												
<i>Oxypolis fendleri</i>												
<i>Oxytropis lambertii</i>												
<i>Pedicularis angustifolia</i>	5	38					<1	100	<1	4		
<i>Pedicularis grayii</i>	<1	8							<1	16		
<i>Pedicularis racemosa</i>	<1	23										
<i>Penstemon barbatus</i>							<1	100				
<i>Penstemon linarioides</i>												
<i>Penstemon oliganthus</i>												
<i>Penstemon pinifolius</i>												
<i>Penstemon whippleanus</i>												
<i>Petalostemon candidum</i>												
<i>Polygonum sawatchensis</i>												
<i>Potentilla crinita</i>												
<i>Potentilla gracilis</i> v <i>pulcher</i>									<1	8		
<i>Potentilla hippiana</i>												
<i>Potentilla</i> spp.												
<i>Potentilla thurberi</i>												
<i>Prunella vulgaris</i>												
<i>Pseudocymopterus montanus</i>												
<i>Pseudostellaria jamesiana</i>	<1	31	<1	50	<1	100			<1	56	<1	20
<i>Psoralea tenuiflora</i>												
<i>Pteridium aquilinum</i>	<1	8	<1	17	<1	100	<1	100	<1	56	2	60
<i>Pterospora andromeda</i>												
<i>Pyrola chlorantha</i>	<1	23	<1	17	<1	100	<1	100	<1	36	<1	20
<i>Pyrola picta</i>	<1	23	<1	17	<1	100	<1	100	<1	4	<1	40
<i>Ramischia secunda</i>	<1	69	<1	83					<1	56	<1	100
<i>Ratibida columnaris</i>												
<i>Rudbeckia laciniata</i>												
<i>Rumex acetosella</i>												
<i>Rumex crispus</i>												
<i>Rumex occidentalis</i>												
<i>Senecio actinella</i>												

(Continued)

Table 2.—(continued).

HTs:	ABLA/VAMY Typic ph. (13)		ABLA/VAMY RUPA ph. (6)		ABLA/LAAR (1)		ABLA/HODU (1)		ABLA/EREX (25)		ABLA/RUPA (5)	
No. plots:	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
Senecio bigelovii	<1	31							<1	28	<1	20
Senecio cardamine			1	17					<1	8	<1	80
Senecio cynthioides												
Senecio eremophilus									<1	4		
Senecio neomexicanus												
Senecio quaerens												
Senecio wootoni	<1	8							1	44		
Sidalcea neomexicana												
Silene lacinata												
Silene scouleri												
Sisymbrium linearifolium												
Smilacina racemosa	<1	23	<1	50			<1	100	<1	32	<1	60
Smilacina stellata	<1	15	<1	33			<1	100	1	60	<1	40
Solidago spathulata var neomex												
Solidago spp.												
Solidago wrightii												
Sphaeralcea coccinea												
Swertia radiata	<1	8	<1	83		<1	100	<1	<1	24	<1	40
Taraxacum spp.												
Thalictrum fendleri						<1	100		<1	36	<1	40
Thermopsis pinetorum			<1	33					<1	8		
Townsendia formosa									<1	4		
Tragia stylaris												
Valeriana capitata			1	33								
Valeriana edulis												
Veratrum californicum												
Verbascum thapsus												
Vicia americana						12	100		<1	56		
Vicia leucophaea												
Vicia pulchella												
Viguiera multiflora												
Viola canadensis	<1	38	<1	67					<1	88	<1	80
Viola nephrophylla											<1	20
Zygadenus elegans			<1	50					<1	8	<1	40
Zygadenus virescens	<1	23							<1	4		

Table 3.—Tree density (D) or shrub-herb cover (C) and constancy (CON) for Apache-Gila-Cibola(Madg.): *Picea pungens* series.

HTs: No. plots:	PIPU/SECA (4)		PIPU/EREX (12)		PIPU/CAFO (6)		PIPU/FEAR (8)		PIPU/POPR (1)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
Trees										
Abies concolor - Young regen.	6	100	10	67			<1	13		
Abies concolor - Advance regen.	2	75	3	50			<1	25		
Abies concolor - Mature	2	75	<1	33						
Abies lasiocarpa - Young regen.	2	50	<1	17	<1	50	<1	25		
Abies lasiocarpa - Advance regen.										
Abies lasiocarpa - Mature	<1	50								
Alnus oblongifolia - Young regen.										
Alnus oblongifolia - Advance regen.										
Alnus oblongifolia - Mature										
Juniperus deppeana - Young regen.										
Juniperus deppeana - Advance regen.										
Juniperus deppeana - Mature										
Juniperus osteosperma - Young regen.										
Juniperus osteosperma - Advance regen.										
Juniperus osteosperma - Mature										
Juniperus scopulorum - Young regen.										
Juniperus scopulorum - Advance regen.										
Juniperus scopulorum - Mature										
Picea engelmannii - Young regen.	2	100	<1	25	4	67	1	13		
Picea engelmannii - Advance regen.	<1	50	<1	17	<1	33	<1	13		
Picea engelmannii - Mature	<1	25	<1	8			<1	13		
Picea pungens - Young regen.	2	75	20	100	12	100	10	100	9	100
Picea pungens - Advance regen.	4	100	9	100	9	100	7	100	22	100
Picea pungens - Mature	2	75	1	58	2	33	3	75	3	100
Pinus edulis - Young regen.										
Pinus edulis - Advance regen.										
Pinus edulis - Mature										
Pinus ponderosa - Young regen.										
Pinus ponderosa - Advance regen.	<1	25	<1	25	1	17	2	75		
Pinus ponderosa - Mature	<1	25	<1	42	3	67	1	88		
Pinus strobiformis - Young regen.	6	100	6	67	3	100	2	63	1	100
Pinus strobiformis - Advance regen.	3	100	3	75	2	33	<1	25		
Pinus strobiformis - Mature			<1	17	<1	17	<1	13		
Populus angustifolia - Young regen.										

(Continued)

Table 3.--(continued).

HTs: No. plots:	PIPU/SECA (4)		PIPU/EREX (12)		PIPU/CAFO (6)		PIPU/FEAR (8)		PIPU/POPR (1)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
Populus angustifolia - Advance regen.										
Populus angustifolia - Mature										
Populus tremuloides - Young regen.										
Populus tremuloides - Advance regen.										
Populus tremuloides - Mature	1	25	<1	25	5	33	1	38		
Pseudotsuga menziesii - Young regen.	9	100	<1	33	2	50	<1	38		
Pseudotsuga menziesii - Advance regen.	8	100	32	100	17	100	17	88		
Pseudotsuga menziesii - Mature	3	75	9	100	9	83	6	63	2	100
Shrubs			3	92	3	67	2	75		
Acer glabrum	<1	25	<1	33			<1	13		
Acer grandidentatum										
Acer negundo										
Alnus oblongifolia										
Berberis repens										
Calliandra humilis										
Ceanothus fendleri							<1	13		
Cercocarpus montanus										
Chimaphila umbellata			<1	8			<1	13		
Cornus stolonifera										
Fraxinus pennsylvanica										
Garrya wrightii										
Gutierrezia sarothrae										
Holodiscus dumosus			<1	8						
Hymenoxys richardsonii			<1	8						
Jamesia americana			<1	8						
Juglans major			<1	8						
Juniperus communis			<1	8	6	50				
Lonicera albiflora										
Lonicera arizonica										
Nolina microcarpa	<1	50	2	33	1	33				
Parthenocissus vitacea										
Philadelphus spp.										
Physocarpus monogynus	<1	50	<1	17						
Populus tremuloides - shrubs	<1	25	<1	42	<1	50	<1	63		

(Continued)

Table 3.—(continued).

HTs: No. plots:	PIPU/SECA (4)		PIPU/EREX (12)		PIPU/CAFO (6)		PIPU/FEAR (8)		PIPU/POPR (1)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
<i>Ptelea trifoliata</i>										
<i>Prunus emarginata</i>			<1	17						
<i>Prunus virginiana</i>										
<i>Quercus chrysolepis</i>										
<i>Quercus emoryi</i>										
<i>Quercus gambelii</i>	<1	25	1	58	<1	17	1	25		
<i>Quercus grisea</i>										
<i>Quercus hypoleucoides</i>										
<i>Quercus rugosa</i>										
<i>Rhamnus betulaeifolia</i>										
<i>Rhus glabra</i>										
<i>Rhus trilobata</i>							<1	13		
<i>Ribes cereum</i>										
<i>Ribes montigenum</i>										
<i>Ribes pinetorum</i>	<1	25	<1	25						
<i>Ribes wolffii</i>			<1	8	<1	17				
<i>Robinia neomexicana</i>	<1	25	<1	17	<1	17				
<i>Rosa</i> spp.	<1	25	<1	58	<1	33	<1	38	1	100
<i>Rubus arizonensis</i>										
<i>Rubus parviflorus</i>	<1	75	<1	58	<1	50	<1	13		
<i>Rubus strigosus</i>	<1	25	<1	33	<1	50	<1	38		
<i>Salix bebbiana</i>										
<i>Salix scouleriana</i>	<1	25	<1	8					<1	100
<i>Salix</i> spp.										
<i>Sambucus</i> spp.										
<i>Shepherdia canadensis</i>					<1	17				
<i>Sorbus dumosa</i>										
<i>Symphoricarpus oreophilus</i>										
<i>Toxicodendron rydbergii</i>										
<i>Vaccinium myrtillus</i>										
<i>Vitis arizonica</i>	<1	25								
<i>Yucca baccata</i>										
<i>Yucca schottii</i>										

(Continued)

Table 3.—(continued).

HTs: No. plots:	PIPU/SECA (4)		PIPU/EREX (12)		PIPU/CAFO (6)		PIPU/FEAR (8)		PIPU/POPR (1)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
Graminoids										
Agropyron arizonicum			<1	17						
Agropyron (smithii?)					<1	17				
Agrostis alba										
Andropogon spp.										
Andropogon cirratus										
Andropogon gerardi										
Andropogon scoparius										
Aristida spp.										
Aristida arizonica										
Aristida fendleriana										
Blepharoneuron tricholepis					<1	17				
Bouteloua curtipendula										
Bouteloua gracilis					<1	17	<1	13		
Bromus anomalus										
Bromus carinatus					<1	50	3	75	6	100
Bromus ciliatus	2	100	5	100						
Bromus frondosus										
Bromus lanatipes										
Bromus spp.					<1	17	<1	13		
Calamagrostis canadensis									20	100
Carex spp.			<1	42			<1	38	2	100
Carex foenea	5	75	3	75	10	100	5	88	40	100
Carex lanuginosa									5	100
Carex microptera										
Carex occidentalis			<1	17						
Carex rossii	1	100	<1	33	1	83	<1	38		
Cyperus rusbyi										
Cyperus sp.										
Elymus glaucus										
Festuca arizonica			<1	17	2	83	9	75		
Festuca sororia										
Glyceria elata			<1	8					<1	100
Glyceria striata									<1	100
Koeleria nitida	<1	50	1	83	<1	67	<1	100		

(Continued)

Table 3.—(continued).

HTs: No. plots:	PIPU/SECA (4)		PIPU/EREX (12)		PIPU/CAFO (6)		PIPU/FEAR (8)		PIPU/POPR (1)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
Luzula parviflora										
Lycurus phleoides										
Melica porteri			<1	8						
Muhlenbergia longiligula										
Muhlenbergia montana			<1	8	<1	17	3	63		
Muhlenbergia monticola										
Muhlenbergia pauciflora										
Muhlenbergia rigens										
Muhlenbergia virescens	<1	25	<1	25	<1	67	1	38		
Muhlenbergia wrightii										
Panicum bulbosum										
Piptochaetium fimbriatum										
Poa compressa										
Poa fendleriana	1	100	1	75	1	50	6	75		
Poa nervosa var tracyi										
Poa pratensis	<1	25	<1	17					25	100
Sitanion hystrix	<1	25	<1	25	<1	17	<1	63		
Sporobolus cryptandrus										
Stipa spp.										
Stipa pringlei			<1	8						
Trisetum montanum	<1	50	<1	17			<1	13		
Forbs										
Achillea millefolium	<1	75	4	92	<1	50	2	88	<1	100
Actaea rubra ssp. arguta			<1	8						
Agrimonia striata										
Allium cernuum			<1	17						
Allium kunthii										
Allium rhizomatum										
Antennaria marginata			<1	25			<1	25		
Antennaria parvifolia			<1	25	<1	17	<1	38		
Antennaria spp.					<1	33				
Aquilegia chrysantha										
Aquilegia elegantula	<1	50	<1	8	<1	17				
Aquilegia triternata	<1	25	<1	25	<1	17				
Arabis spp.					<1	17				

(Continued)

Table 3.—(continued).

HTs: No. plots:	PIPU/SECA (4)		PIPU/EREX (12)		PIPU/CAFO (6)		PIPU/FEAR (8)		PIPU/POPR (1)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
<i>Arenaria lanuginosa</i>			<1	25			<1	13		
<i>Arenaria</i> spp.					<1	67	<1	38		
<i>Artemisia carruthii</i>										
<i>Artemisia dracunculoides</i>										
<i>Artemisia franserioides</i>			2	50			<1	38		
<i>Artemisia frigida</i>										
<i>Artemisia ludoviciana</i>			<1	17			<1	38		
<i>Asclepias</i> spp.										
<i>Aster falcatus</i>										
<i>Astragalus egglesonii</i>										
<i>Astragalus gilensis</i>										
<i>Astragalus humistratus</i>										
<i>Astragalus</i> spp.										
<i>Bahia dissecta</i>										
<i>Brickellia brachyphylla</i>										
<i>Brickellia fendleri</i>			<1	8						
<i>Brickellia grandiflora</i>										
<i>Brickellia</i> spp.										
<i>Calypso bulbosa</i>										
<i>Campanula rotundifolia</i>			<1	58	<1	50	<1	38		
<i>Cardamine cordifolia</i>			<1	8						
<i>Castilleja</i> spp.			<1	42			<1	25		
<i>Chaptalia alsophila</i>		<1	<1	33			<1	13		
<i>Chamerion angustifolium</i>			<1	8						
<i>Cicuta douglasii</i>									2	100
<i>Circaea alpina</i>			<1	8					3	100
<i>Cirsium</i> spp.			<1	17	<1	33	<1	38		
<i>Cirsium parryi</i>			<1	33					<1	100
<i>Cirsium wheeleri</i>										
<i>Clematis ligusticifolia</i>			<1	8			<1	13		
<i>Clematis pseudoalpina</i>			<1	42			<1	25		
<i>Cologania longifolia</i>		<1								
<i>Commelina dianthifolia</i>										
<i>Corallorhiza</i> spp.										
<i>Corallorhiza maculata</i>			<1	8	<1	17				

(Continued)

Table 3.—(continued).

HTs: No. plots:	PIPU/SECA (4)		PIPU/EREX (12)		PIPU/CAFO (6)		PIPU/FEAR (8)		PIPU/POPR (1)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
<i>Cryptantha jamesii</i>										
<i>Cucurbita foetidissima</i>										
<i>Cystopteris fragilis</i>	<1	50	<1	58			<1	13		
<i>Delphinium tenuisectum</i>										
<i>Desmanthus cooleyi</i>	<1	25								
<i>Disporum trachycarpum</i>										
<i>Draba helleriana</i>			<1	42			<1	25		
<i>Dugaldia hoopesii</i>	<1	25	1	50	<1	17	<1	13	2	100
<i>Equisetum arvense</i>										
<i>Equisetum laevigatum</i>										
<i>Erigeron concinnus</i>										
<i>Erigeron delphinifolius</i>										
<i>Erigeron divergens</i>										
<i>Erigeron eximius</i>	<1	50	12	75	<1	83	<1	63		
<i>Erigeron flagellaris</i>							<1	13		
<i>Erigeron formosissimus</i>			1	17			<1	38		
<i>Erigeron platyphyllus</i>							<1	13		
<i>Eriogonum alatum</i>										
<i>Eriogonum jamesii</i>										
<i>Erysimum capitatum</i>										
<i>Fragaria americana</i>	6	100	5	83	3	17	<1	25		
<i>Fragaria ovalis</i>	<1	75	2	83	1	83	3	75	<1	100
<i>Galium</i> spp.										
<i>Galium fendleri</i>			<1	8						
<i>Galium mexicanum</i>										
<i>Gaura hexandra</i>										
<i>Gentianella amarella</i> s. <i>acuta</i>			<1	33						
<i>Geranium caespitosum</i>			<1	8	<1	17				
<i>Geranium richarsonii</i>	<1	100	5	75	<1	50	2	50	1	100
<i>Geranium</i> spp.			<1	8	<1	17	2	13		
<i>Geum aleppicum</i> ssp. <i>strictum</i>			<1	8					15	100
<i>Gnaphalium macounii</i>										
<i>Goodyera oblongifolia</i>	<1	25	<1	8			<1	13		
<i>Goodyera repens</i>			<1	17						
<i>Halenia recurva</i>			<1	17						

(Continued)

Table 3.—(continued).

HTs: No. plots:	PIPU/SECA (4)		PIPU/EREX (12)		PIPU/CAFO (6)		PIPU/FEAR (8)		PIPU/POPR (1)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
Haplopappus parryi	<1	25	<1	50	<1	50	<1	50		
Hedeoma oblongifolium										
Hedyotis pygmaea										
Helianthella parryi										
Heterotheca fulcrata										
Hieracium fendleri			<1	42						
Hydrophyllum fendleri										
Hymenopappus filifolius										
Hymenopappus mexicanus										
Hypericum formosum			<1	8					4	100
Ipomopsis aggregata			<1	8	<1	17				
Iris missouriensis			<1	17					1	100
Kuhnia chlorolepis										
Lactuca graminifolia										
Lathyrus arizonicus	5	100	1	58	5	83	4	63		
Lathyrus graminifolius							<1	13		
Leucelene ericoides										
Ligusticum porteri			<1	25						
Linum lewisii										
Lithospermum multiflorum	<1	50	<1	25	<1	17	<1	50		
Lobelia anatina										
Lotus wrightii										
Lupinus neomexicanus										
Lupinus spp.			<1		<1	17	<1	13		
Malaxis ehrenbergii										
Malaxis soulei										
Mertensia franciscana			<1	25						
Monarda menthaefolia										
Opuntia spp. (prickly pears)										
Osmorhiza depauperata	<1	25	<1	42						
Oxalis metcalfei	<1	25	<1	58			<1	13		
Oxybaphus linearis										
Oxypolis fendleri			<1	8					2	100
Oxytropis lambertii			<1							
Pedicularis angustifolia			<1	17						

(Continued)

Table 3.—(continued).

HTs: No. plots:	PIPU/SECA (4)		PIPU/EREX (12)		PIPU/CAFO (6)		PIPU/FEAR (8)		PIPU/POPR (1)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
<i>Pedicularis grayii</i>	<1	50								
<i>Pedicularis racemosa</i>										
<i>Penstemon barbatus</i>	<1	50	<1	25			<1	63		
<i>Penstemon linarioides</i>										
<i>Penstemon oliganthus</i>										
<i>Penstemon pinifolius</i>										
<i>Penstemon whippleanus</i>										
<i>Petalostemon candidum</i>										
<i>Polygonum sawatchensis</i>										
<i>Potentilla crinita</i>							<1	13		
<i>Potentilla gracilis v pulcher</i>			<1	17	<1	33	<1	38		
<i>Potentilla hippiana</i>			<1	25			<1	13		
<i>Potentilla spp.</i>			<1	8						
<i>Potentilla thurberi</i>		25	<1	42						
<i>Prunella vulgaris</i>	<1	25	<1	33						
<i>Pseudocymopterus montanus</i>			2	75						
<i>Pseudostellaria jamesiana</i>	<1	25	<1	67	<1	38				
<i>Psoralea tenuiflora</i>										
<i>Pteridium aquilinum</i>	<1	50	<1	42	<1	17	1	25		
<i>Pterospora andromeda</i>			<1	8						
<i>Pyrola chlorantha</i>	<1	25	<1	17						
<i>Pyrola picta</i>										
<i>Ramischia secunda</i>	<1	50	<1	8						
<i>Ratibida columnaris</i>										
<i>Rudbeckia laciniata</i>									6	100
<i>Rumex acetosella</i>			<1	8					<1	100
<i>Rumex crispus</i>										
<i>Rumex occidentalis</i>									<1	100
<i>Senecio actinella</i>										
<i>Senecio bigelovii</i>			3	50			<1	13		
<i>Senecio cardamine</i>	9	100					<1	13		
<i>Senecio cynthioides</i>			<1	8						
<i>Senecio eremophilus</i>	<1	25	<1	17						
<i>Senecio neomexicanus</i>			<1	33	<1	83	<1	88		
<i>Senecio quaerens</i>			<1	17						

(Continued)

Table 3.--(continued).

HTs: No. plots:	PIPU/SECA (4)		PIPU/EREX (12)		PIPU/CAFO (6)		PIPU/FEAR (8)		PIPU/POPR (1)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
<i>Senecio wootoni</i>	2	100	1	58	3	83	2	63	4	100
<i>Sidalcea neomexicana</i>										
<i>Silene lacinata</i>	<1	50			<1	17				
<i>Silene scouleri</i>	<1	25	<1	25						
<i>Sisymbrium linearifolium</i>										
<i>Smilacina racemosa</i>	<1	75	<1	58	<1	17	<1	25		
<i>Smilacina stellata</i>	<1	25	<1	25	<1	67	1	50	1	100
<i>Solidago spathulata</i> var <i>neomex</i>										
<i>Solidago</i> spp.			<1	8			<1	38		
<i>Solidago wrightii</i>										
<i>Sphaeralcea coccinea</i>										
<i>Swertia radiata</i>			<1	33	<1	17	<1	13		
<i>Taraxacum</i> spp.			<1	17	<1	33	<1	25		
<i>Thalictrum fendleri</i>	2	75	<1	67	<1	67	2	63		
<i>Thermopsis pinetorum</i>	15	75	<1	17						
<i>Townsendia formosa</i>			<1	25	<1	33	<1	38		
<i>Tragia stylaris</i>										
<i>Valeriana capitata</i>			2	33	<1	17	2	38		
<i>Valeriana edulis</i>			<1	33						
<i>Veratrum californicum</i>			<1	8						
<i>Verbascum thapsus</i>										
<i>Vicia americana</i>			<1	42	<1	83	<1	75	1	100
<i>Vicia leucophaea</i>										
<i>Vicia pulchella</i>										
<i>Viguiera multiflora</i>										
<i>Viola canadensis</i>	2	100	1	100	<1	50	<1	38		
<i>Viola nephrophylla</i>			<1	8					<1	100
<i>Zygadenus elegans</i>			<1	25						
<i>Zygadenus virescens</i>										

Table 4.—Tree density (D) or shrub-herb cover (C) and constancy (CON) for Apache-Gila-Cibola (Madg.): *Abies concolor* series.

HTs:	ABCO/ EREX	ABCO/ Sparse	ABCO/ HODU	ABCO/ ACGL	ABCO/ MUVI	ABCO/ QUGA Typic ph. MUVI ph.	ABCO/ QUGA (19)	ABCO/ QUGA (8)	ABCO/ RONE	ABCO/ FEAR Typic ph. POFE ph.	ABCO/ FEAR (3)	ABCO/ ACGR	ABCO/ JUMA											
No. plots:	(10)	(20)	(3)	(13)	(5)	(19)	(8)	(2)	(4)	(3)	(1)	(1)	(1)											
	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON											
Trees																								
<i>Abies concolor</i> - Young regen.	> 100	100	30	100	20	100	25	92	33	100	16	95	7	75	23	50	37	100	24	100	40	100	55	100
<i>Abies concolor</i> - Advance regen.	7	100	12	100	5	67	10	85	9	100	5	95	4	75	19	50	10	75	16	100	4	100	1	100
<i>Abies concolor</i> - Mature	3	100	3	80	1	67	5	92	1	60	2	63	<1	13	3	50	1	75	2	100	2	100	1	100
<i>Abies lasiocarpa</i> - Young regen.			<1	25			<1	8																
<i>Abies lasiocarpa</i> - Advance regen.			<1	10			<1	8																
<i>Abies lasiocarpa</i> - Mature																								
<i>Alnus oblongifolia</i> - Young regen.																								
<i>Alnus oblongifolia</i> - Advance regen.																								
<i>Alnus oblongifolia</i> - Mature																								
<i>Juniperus deppeana</i> - Young regen.																								
<i>Juniperus deppeana</i> - Advance regen.																								
<i>Juniperus deppeana</i> - Mature																								
<i>Juniperus osteosperma</i> - Young regen.																								
<i>Juniperus osteosperma</i> - Advance regen.																								
<i>Juniperus osteosperma</i> - Mature																								
<i>Juniperus scopulorum</i> - Young regen.																								
<i>Juniperus scopulorum</i> - Advance regen.																								
<i>Juniperus scopulorum</i> - Mature																								
<i>Picea engelmannii</i> - Young regen.			2	15																				
<i>Picea engelmannii</i> - Advance regen.	<1	10	<1	20																				
<i>Picea engelmannii</i> - Mature	<1	10																						
<i>Picea pungens</i> - Young regen.																								
<i>Picea pungens</i> - Advance regen.																								
<i>Picea pungens</i> - Mature																								
<i>Pinus edulis</i> - Young regen.																								
<i>Pinus edulis</i> - Advance regen.																								
<i>Pinus edulis</i> - Mature																								
<i>Pinus ponderosa</i> - Young regen.	1	20	<1	30	<1	33	<1	23	2	60	1	42	4	63	2	50	1	50	<1	33				
<i>Pinus ponderosa</i> - Advance regen.			<1	30	3	67	<1	23	3	20	2	42	4	63			3	100						
<i>Pinus ponderosa</i> - Mature	<1	10	1	55	<1	33	<1	8	2	100	1	53	4	88	<1	50	1	25	<1	67				
<i>Pinus strobfiformis</i> - Young regen.	7	100	6	85	8	100	6	100	4	100	3	63	5	88	<1	50	3	75	4	100				
<i>Pinus strobfiformis</i> - Advance regen.	2	70	2	80	<1	33	2	62	2	80	2	63	2	75	<1	50	4	75	<1	33				
<i>Pinus strobfiformis</i> - Mature	<1	50	<1	50			1	46	<1	40	1	58	<1	50										
<i>Populus angustifolia</i> - Young regen.																								
<i>Populus angustifolia</i> - Advance regen.																								
<i>Populus angustifolia</i> - Mature																								
<i>Populus tremuloides</i> - Young regen.																								
<i>Populus tremuloides</i> - Advance regen.	5	70	<1	20	6	67	1	46	<1	20														
<i>Populus tremuloides</i> - Mature	3	60	<1	15			<1	15	1	40	<1	5					4	50						
<i>Pseudotsuga menziesii</i> - Young regen.	32	100	29	95	11	100	21	100	23	100	20	100	9	75	2	50	18	100	17	100	25	100	1	100
<i>Pseudotsuga menziesii</i> - Advance regen.	5	90	7	100	4	67	10	92	8	80	10	95	6	100	6	50	11	100	5	100	3	100	7	100
<i>Pseudotsuga menziesii</i> - Mature	6	100	4	100	4	100	3	77	4	100	2	79	<1	38	1	50	2	50	3	100	1			

(Continued)

(Continued)

Table 4.—(continued).

HTs:	ABCO/ EREX	ABCO/ Sparse	ABCO/ HODU	ABCO/ ACGL	ABCO/ MUVI	ABCO/ QUGA Typic ph. (19)	ABCO/ QUGA MUVI ph. (8)	ABCO/ RONE D/C CON	ABCO/ FEAR Typic ph. (4)	ABCO/ FEAR POFE ph. (3)	ABCO/ ACGR	ABCO/ JUMA
No. plots:	(10)	(20)	(3)	(13)	(5)	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
Shrubs	11	60	<1	25	8	100	<1	5			18	100
Acer glabrum											5	100
Acer grandidentatum												
Acer negundo												
Alnus oblongifolia		<1	15				<1	5				
Berberis repens												
Calliandra humilis		<1	5				<1	5				
Ceanothus fendleri												
Cercocarpus montanus							<1	5				
Chimaphila umbellata							<1	5				
Cornus stolonifera	<1	10	<1	35			<1	23		<1	33	
Fraxinus pennsylvanica												
Garrya wrightii												1
Gutierrezia sarothrae												100
Holodiscus dumosus	<1	10	<1	5	2	67	1	62				
Hymenoxys richardsonii												
Jamesia americana					6	100	<1	23				
Juglans major												30
Juniperus communis												100
Lonicera albiflora												
Lonicera arizonica	<1	10	<1	35	1	33	2	54				
Nolina microcarpa												
Parthenocissus vitacea												
Philadelphus spp.												
Physocarpus monogynus		<1	20				<1	54				
Populus tremuloides - shrubs	2	70	<1	45	<1	67	<1	15				
Ptelea trifoliata												
Prunus emarginata												
Prunus virginiana												
Quercus chrysolepis												
Quercus emoryi												
Quercus gambelii	<1	30	<1	30			<1	23				
Quercus grisea												
Quercus hypoleucoides												
Quercus rugosa												
Rhamnus betulaeifolia												
Rhus glabra												
Rhus trilobata												
Ribes cereum												
Ribes montigenum												
Ribes pinetorum	<1	40										
Ribes wolffii												
Robinia neomexicana	<1	10	<1	65								

(Continued)

Table 4.--(continued).

HTs:	ABCO/ EREX	ABCO/ Sparse	ABCO/ HODU	ABCO/ ACGL	ABCO/ MUVI	ABCO/ QUGA Typic ph. MUVI ph. (19)	ABCO/ QUGA (8)	ABCO/ RONE (2)	ABCO/ FEAR Typic ph. POFE ph. (4)	ABCO/ FEAR (3)	ABCO/ ACGR	ABCO/ JUMA
No. plots:	(10)	(20)	(3)	(13)	(5)	(19)	(8)	(2)	D/C CON	D/C CON	D/C CON	D/C CON
	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
Rosa spp.	<1	20	<1	15	<1	23	<1	40	<1	37	<1	50
Rubus arizonensis	<1	20	<1	15	<1	23	<1	40	<1	37	<1	50
Rubus parviflorus	<1	10	<1	30	<1	15	<1	20	<1	5	<1	67
Rubus strigosus	<1	10	<1	30	<1	15	<1	20	<1	5	<1	67
Salix bebbiana	<1	10	<1	15	<1	23	<1	5	<1	67	<1	67
Salix scouleriana	<1	10	<1	15	<1	23	<1	5	<1	67	<1	67
Salix spp.	<1	10	<1	15	<1	23	<1	5	<1	67	<1	67
Sambucus spp.	<1	10	<1	15	<1	23	<1	5	<1	67	<1	67
Shepherdia canadensis	<1	10	<1	15	<1	23	<1	5	<1	67	<1	67
Sorbus dumosa	<1	10	<1	15	<1	23	<1	5	<1	67	<1	67
Symphoricarpus oreophilus	<1	10	<1	60	<1	15	<1	13	<1	67	<1	67
Toxicodendron rydbergii	<1	10	<1	60	<1	15	<1	13	<1	67	<1	67
Vaccinium myrtillus	<1	10	<1	60	<1	15	<1	13	<1	67	<1	67
Vitis arizonica	<1	10	<1	60	<1	15	<1	13	<1	67	<1	67
Yucca baccata	<1	10	<1	60	<1	15	<1	13	<1	67	<1	67
Yucca schottii	<1	10	<1	60	<1	15	<1	13	<1	67	<1	67
Graminoids												
Agropyron arizonicum	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Agropyron (smithii?)	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Agrostis alba	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Andropogon spp.	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Andropogon cirratus	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Andropogon gerardi	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Andropogon scoparius	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Aristida spp.	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Aristida arizonica	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Aristida fendleriana	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Blepharoneuron tricholepis	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Bouteloua curtipendula	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Bouteloua gracilis	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Bromus anomalus	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Bromus carinatus	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Bromus ciliatus	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Bromus frondosus	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Bromus lanatipes	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Bromus spp.	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Calamagrostis canadensis	3	70	<1	5	<1	11	<1	5	<1	13	<1	13
Carex spp.	<1	50	<1	20	<1	33	<1	8	<1	60	<1	37
Carex foenea	<1	50	<1	20	<1	33	<1	8	<1	60	<1	37
Carex lanuginosa	13	70	<1	20	<1	33	<1	8	<1	60	<1	37
Carex microptera	<1	50	<1	20	<1	33	<1	8	<1	60	<1	37
Carex occidentalis	<1	50	<1	20	<1	33	<1	8	<1	60	<1	37

(Continued)

Table 4.--(continued).

HTs:	ABCO/ EREX	(10)	ABCO/ Sparse	(20)	ABCO/ HODU	(3)	ABCO/ ACGL	(13)	ABCO/ MUUVI	(5)	ABCO/ Typic ph. MUUVI	(19)	ABCO/ QUGA	(8)	ABCO/ RONE	(2)	ABCO/ Typic ph. MUUVI	(4)	ABCO/ FEAR	(3)	ABCO/ POFE ph.	(1)	ABCO/ JUMA	(1)
No. plots:	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
<i>Carex rossii</i>	<1	10	<1	40	<1	38	<1	40	<1	37	<1	63	1	50	<1	25	1	67						
<i>Cyperus rusbyi</i>																								
<i>Elymus glaucus</i>																								
<i>Festuca arizonica</i>																								
<i>Festuca sororia</i>	2	40	<1	5	1	67	<1	8																
<i>Glyceria elata</i>																								
<i>Glyceria striata</i>																								
<i>Koeleria nitida</i>	<1	40	<1	35	2	100	<1	38	<1	60	1	74	<1	75	<1	50	3	75	<1	33				
<i>Luzula parviflora</i>																								
<i>Lycurus phleoides</i>																								
<i>Melica porteri</i>																								
<i>Muhlenbergia longiligula</i>																								
<i>Muhlenbergia montana</i>																								
<i>Muhlenbergia monticola</i>																								
<i>Muhlenbergia pauciflora</i>																								
<i>Muhlenbergia rigens</i>																								
<i>Muhlenbergia virescens</i>	<1	10	<1	25			<1	8	5	100	<1	42	14	100			<1	33						
<i>Muhlenbergia wrightii</i>																								
<i>Panicum bulbosum</i>																								
<i>Piptochaetium fimbriatum</i>																								
<i>Poa compressa</i>																								
<i>Poa fendleriana</i>	<1	50	<1	35	<1	33	<1	62	<1	100	3	100	<1	75	<1	50	4	50	12	100	<1	100	<1	100
<i>Poa nervosa</i> var <i>tracyi</i>																								
<i>Poa pratensis</i>																								
<i>Sitanion hystrix</i>	<1	10	<1	30	<1	67	<1	8	1	60	<1	42	<1	75			<1	75	<1	33				
<i>Sporobolus cryptandrus</i>																								
<i>Stipa spp.</i>																								
<i>Stipa pringlei</i>	<1	40	<1	5			<1	8																
<i>Trisetum montanum</i>																								
Forbs																								
<i>Achillea millefolium</i>																								
<i>Actaea rubra</i> ssp. <i>arguta</i>	2	80	<1	20	<1	67	<1	23	<1	80	2	68	1	75	<1	50	<1	75	<1	67				
<i>Agrimonia striata</i>																								
<i>Allium cernuum</i>																								
<i>Allium kunthii</i>																								
<i>Allium rhizomatum</i>																								
<i>Antennaria marginata</i>																								
<i>Antennaria parvifolia</i>	<1	20	<1	5	<1	33	<1	8			<1	21					2	50						
<i>Antennaria</i> spp.																								
<i>Aquilegia chrysantha</i>	<1	10	<1	10	<1	10	<1	8			<1	16	<1	13			<1	25						
<i>Aquilegia elegantula</i>	<1	10	<1	5							<1	16	<1	25			<1	25						
<i>Aquilegia triternata</i>	<1	20	<1	5																				

(Continued)

Table 4.—(continued).

HTs:	ABCO/ EREX	ABCO/ Sparse	ABCO/ HODU	ABCO/ ACGL	ABCO/ MUVI	ABCO/ QUGA Typic ph. (19)	ABCO/ MUVI ph. (8)	ABCO/ RONE	ABCO/ FEAR Typic ph. (4)	ABCO/ FEAR POFE ph. (3)	ABCO/ ACGR	ABCO/ JUMA
No. plots:	(10)	(20)	(3)	(13)	(5)	D/C CON	D/C CON	(2)	D/C CON	D/C CON	(1)	(1)
D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
<i>Arabis</i> spp.	<1	10	<1	5	<1	5	<1	5	<1	5	<1	5
<i>Arenaria lanuginosa</i>	<1	10	<1	5	<1	5	<1	5	<1	5	<1	5
<i>Arenaria</i> spp.	<1	10	<1	5	<1	5	<1	5	<1	5	<1	5
<i>Artemisia carruthii</i>	<1	10	<1	5	<1	5	<1	5	<1	5	<1	5
<i>Artemisia dracunculoides</i>	<1	10	<1	5	<1	5	<1	5	<1	5	<1	5
<i>Artemisia franserioides</i>	2	70	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Artemisia frigida</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Artemisia ludoviciana</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Asclepias</i> spp.	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Aster falcatus</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Astragalus egglestonii</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Astragalus gilensis</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Astragalus humistratus</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Astragalus</i> spp.	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Bahia dissecta</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Brickellia brachyphylla</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Brickellia fendleri</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Brickellia grandiflora</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Brickellia</i> spp.	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Calypso bulbosa</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Campanula rotundifolia</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Cardamine cordifolia</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Castilleja</i> spp.	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Chaptalia alsophila</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Chamerion angustifolium</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Cicuta douglasii</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Circaea alpina</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Cirsium</i> spp.	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Cirsium parryi</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Cirsium wheeleri</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Clematis ligusticifolia</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Clematis pseudoalpina</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Cologania longifolia</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Commelina dianthifolia</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Corallorhiza</i> spp.	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Corallorhiza maculata</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Cryptantha jamesii</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Cucurbita foetidissima</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Cystopteris fragilis</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Delphinium tenuisectum</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Desmanthus cooleyi</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Disporum trachycarpum</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11
<i>Draba helleriana</i>	<1	20	<1	5	<1	33	<1	46	<1	20	<1	11

(Continued)

Table 4.--(continued).

HTs:	ABCO/ EREX	ABCO/ Sparse	ABCO/ HODU	ABCO/ ACGL	ABCO/ MUUVI	ABCO/ QUGA Typic ph.	ABCO/ QUGA MUUVI ph.	ABCO/ RONE	ABCO/ FEAR Typic ph.	ABCO/ FEAR POFE ph.	ABCO/ ACGR	ABCO/ JUMA
No. plots:	(10)	(20)	(3)	(13)	(5)	(19)	(8)	(2)	(4)	(3)	(1)	(1)
D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
Dugaldia hoopesii	2	50	<1	15	<1	40	<1	5	<1	13	<1	33
Equisetum arvense												
Equisetum laevigatum												
Erigeron concinnus												
Erigeron delphinifolius												
Erigeron divergens												
Erigeron eximius	10	70	<1	5	<1	33	<1	38	<1	50	<1	67
Erigeron flagellaris												
Erigeron formosissimus												
Erigeron platyphyllus	<1	10										
Erigonum alatum												
Erigonum jamesii												
Erysimum capitatum												
Fragaria americana	<1	40	<1	20	<1	62	<1	25	<1	50	3	100
Fragaria ovalis	1	80	<1	45	<1	33	<1	23	<1	50	<1	67
Galium spp.												
Galium fendleri												
Galium mexicanum												
Gaura hexandra												
Gentianella amarella s. acuta	<1	10										
Geranium caespitosum	<1	10	<1	5	<1	40	<1	42	<1	100	<1	100
Geranium richardsonii	5	100	<1	45	<1	38	<1	20	<1	50	<1	100
Geranium spp.												
Geum aleppicum ssp. strictum												
Gnaphalium macounii												
Goodyera oblongifolia	<1	20	<1	50	<1	8	<1	40	<1	5		
Goodyera repens	<1	10	<1	5	<1	8	<1	5				
Halenia recurva												
Haplopappus parryi	<1	80	<1	60	<1	67	<1	54	<1	67	<1	67
Hedeoma oblongifolium												
Hedyotis pygmaea												
Helianthella parryi												
Heterotheca fulcrata												
Hieracium fendleri	<1	10	<1	10	<1	8	<1	40	<1	11	<1	38
Hydrophyllum fendleri												
Hymenopappus filifolius												
Hymenopappus mexicanus												
Hypericum formosum												
Ipomopsis aggregata												
Iris missouriensis												
Kuhnia chlorolepis												
Lactuca graminifolia												
Lathyrus arizonicus	4	80	<1	55	<1	46	2	80	2	63	<1	75

(Continued)

Table 4.—(continued).

HTs:	ABCO/ EREX	ABCO/ Sparse	ABCO/ HODU	ABCO/ ACGL	ABCO/ MUVI	ABCO/ QUGA Typic ph. (19)	ABCO/ QUGA MUVI ph. (8)	ABCO/ RONE D/C CON	ABCO/ FEAR Typic ph. (4)	ABCO/ FEAR POFE ph. (3)	ABCO/ ACGR	ABCO/ JUMA
No. plots:	(10)	(20)	(3)	(13)	(5)	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
Lathyrus graminifolius	<1	60	<1	20	<1	21	<1	13				
Leucelene ericoides												
Ligusticum porteri												
Linum lewisii												
Lithospermum multiflorum												
Lobelia anatina												
Lotus wrightii												
Lupinus neomexicanus												
Lupinus spp.												
Malaxis ehrenbergii												
Malaxis soulei												
Mertensia franciscana												
Monarda menthaefolia												
Opuntia spp. (prickly pears)												
Osmorhiza depauperata												
Oxalis metcalfei												
Oxybaphus linearis												
Oxytropis fendleri												
Oxytropis lambertii												
Pedicularis angustifolia												
Pedicularis grayii												
Pedicularis racemosa												
Penstemon barbatus												
Penstemon linarioides												
Penstemon oliganthus												
Penstemon pinifolius												
Penstemon whippleanus												
Petalostemon candidum												
Polygonum sawatchensis												
Potentilla crinita												
Potentilla gracilis v pulcher												
Potentilla hippiana												
Potentilla spp.												
Potentilla thurberi												
Prunella vulgaris												
Pseudocymopterus montanus												
Pseudostellaria jamesiana												
Psoralea tenuiflora												
Pteridium aquilinum												
Pterospora andromeda												
Pyrola chlorantha												
Pyrola picta												

(Continued)

Table 4.--(continued).

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Table 5.—Tree density (D) or shrub-herb cover (C) and constancy (CON) for Apache-Gila-Cibola (Madg.): *Pseudotsuga menziesii* series.

HTs:	PSME/ ARUV	PSME/ HODU	PSME/ FEAR	PSME/ BRCI	PSME/ QUGA Typic ph. (27)	PSME/ QUGA MUVI ph. (10)	PSME/ QUGA FEAR ph. (2)	PSME/ MUVI	PSME/ MUMO	PSME/ QUHY
No. plots:	(2)	(1)	(9)	(8)	D/C CON	D/C CON	D/C CON	(9)	(7)	(7)
	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
Trees										
Abies concolor - Young regen.			<1	<1	13	<1	11	<1	10	<1
Abies concolor - Advance regen.			<1	11		<1	4	<1	30	
Abies concolor - Mature										
Abies lasiocarpa - Young regen.										
Abies lasiocarpa - Advance regen.										
Abies lasiocarpa - Mature										
Alnus oblongifolia - Young regen.										
Alnus oblongifolia - Advance regen.										
Alnus oblongifolia - Mature										
Juniperus deppeana - Young regen.										
Juniperus deppeana - Advance regen.										
Juniperus deppeana - Mature										
Juniperus osteosperma - Young regen.										
Juniperus osteosperma - Advance regen.										
Juniperus osteosperma - Mature										
Juniperus scopulorum - Young regen.										
Juniperus scopulorum - Advance regen.										
Juniperus scopulorum - Mature										
Picea engelmannii - Young regen.			<1	11	13					
Picea engelmannii - Advance regen.			<1	11	<1					
Picea engelmannii - Mature										
Picea pungens - Young regen.										
Picea pungens - Advance regen.										
Picea pungens - Mature										
Pinus edulis - Young regen.			<1	22						
Pinus edulis - Advance regen.										
Pinus edulis - Mature										
Pinus ponderosa - Young regen.			4	56						
Pinus ponderosa - Advance regen.	2	50	2	44						
Pinus ponderosa - Mature			3	78						
Pinus strobfiformis - Young regen.	29	100	5	67	6	100	4	56	3	70
Pinus strobfiformis - Advance regen.	6	100	3	78	2	75	1	48	2	50
Pinus strobfiformis - Mature	2	100	1	44	2	75	<1	22	<1	20
Populus angustifolia - Young regen.										
Populus angustifolia - Advance regen.										
Populus angustifolia - Mature										
Populus tremuloides - Young regen.	8	100	1	22						
Populus tremuloides - Advance regen.			<1	22						
Populus tremuloides - Mature										
Pseudotsuga menziesii - Young regen.	16	100	3	100	30	100	26	100	12	100
Pseudotsuga menziesii - Advance regen.	4	100	7	89	8	88	12	100	6	80
Pseudotsuga menziesii - Mature	3	100	6	100	9	100	3	81	<1	20

(Continued)

Table 5.—(continued).

HTs:	PSME/ ARUV	PSME/ HODU	PSME/ FEAR	PSME/ BRCI	PSME/ QUGA (27)	PSME/ QUGA MUVI ph. (10)	PSME/ QUGA FEAR ph. (2)	PSME/ MUVI	PSME/ MUMO	PSME/ QUHY
No. plots:	(2) D/C CON	(1) D/C CON	(9) D/C CON	(8) D/C CON	D/C CON	D/C CON	D/C CON	(9) D/C CON	(7) D/C CON	(7) D/C CON
Shrubs										
<i>Acer glabrum</i>				1 38	1 7					
<i>Acer grandidentatum</i>										
<i>Acer negundo</i>										
<i>Alnus oblongifolia</i>					<1 26	<1 10				
<i>Berberis repens</i>										
<i>Calliandra humilis</i>					<1 7	<1 40			14	<1 43
<i>Ceanothus fendleri</i>			<1 11		<1 7				29	1 71
<i>Cercocarpus montanus</i>							<1 50			<1 29
<i>Chimaphila umbellata</i>										
<i>Cornus stolonifera</i>										
<i>Fraxinus pennsylvanica</i>					<1 7					<1 14
<i>Garrya wrightii</i>					<1 4					<1 14
<i>Gutierrezia sarothrae</i>										
<i>Holodiscus dumosus</i>					<1 7					
<i>Hymenoxys richardsonii</i>										
<i>Jamesia americana</i>	<1 50	5 100	<1 33	1 63	<1 7		<1 50	<1 11	<1 29	<1 14
<i>Juglans major</i>				<1 25						
<i>Juniperus communis</i>	1 100									
<i>Lonicera albiflora</i>										
<i>Lonicera arizonica</i>	<1 50				<1 33				<1 14	<1 14
<i>Nolina microcarpa</i>										
<i>Parthenocissus vitacea</i>										
<i>Philadelphus</i> spp.					<1 4				<1 14	
<i>Physocarpus monogynus</i>				<1 13						
<i>Populus tremuloides</i> - shrubs	<1 100		<1 22	<1 63		<1 30		<1 22		
<i>Ptelea trifoliata</i>					<1 4					
<i>Prunus emarginata</i>					<1 4	<1 20				
<i>Prunus virginiana</i>					<1 4	<1 10				
<i>Quercus chrysolepis</i>					<1 4					
<i>Quercus emoryi</i>										
<i>Quercus gambelii</i>			<1 33		30 100	23 100	25 100	<1 33	2 57	4 43
<i>Quercus grisea</i>			<1 11				3 50	<1 11	1 14	1 29
<i>Quercus hypoleucoides</i>									<1 14	18 86
<i>Quercus rugosa</i>										18 100
<i>Rhamnus betulaeifolia</i>										
<i>Rhus glabra</i>									<1 14	
<i>Rhus trilobata</i>										
<i>Ribes cereum</i>			<1 22	<1 25						
<i>Ribes montigenum</i>										
<i>Ribes pinetorum</i>			<1 22	1 50						
<i>Ribes wolffii</i>										

(Continued)

Table 5.--(continued).

HTs:	PSME/ ARUV	PSME/ HODU	PSME/ FEAR	PSME/ BRCI	PSME/ QUGA Typic ph. (27)	PSME/ QUGA MUVI ph. (10)	PSME/ QUGA FEAR ph. (2)	PSME/ MUVI	PSME/ MUMO	PSME/ QUHY
No. plots:	(2) D/C CON	(1) D/C CON	(9) D/C CON	(8) D/C CON	D/C CON	D/C CON	D/C CON	(9) D/C CON	(7) D/C CON	(7) D/C CON
<i>Robinia neomexicana</i>		4 100		<1 13	<1 44	1 30		<1 22	<1 14	<1 43
<i>Rosa</i> spp.					<1 44	<1 30		<1 33	<1 14	
<i>Rubus arizonensis</i>										
<i>Rubus parviflorus</i>										
<i>Rubus strigosus</i>										
<i>Salix bebbiana</i>										
<i>Salix scouleriana</i>		2 100			<1 4					
<i>Salix</i> spp.					<1 4					
<i>Sambucus</i> spp.									<1 14	
<i>Shepherdia canadensis</i>										
<i>Sorbus dumosa</i>										
<i>Symphoricarpos oreophilus</i>		6 100		<1 13	<1 15	<1 10		<1 11	<1 14	
<i>Toxicodendron rydbergii</i>					<1 4			<1 11		
<i>Vaccinium myrtillus</i>										
<i>Vitis arizonica</i>										
<i>Yucca baccata</i>				<1 4					<1 14	14
<i>Yucca schottii</i>										
Graminoids										
<i>Agropyron arizonicum</i>					<1 7					
<i>Agropyron (smithii?)</i>										
<i>Agrostis alba</i>									<1 14	
<i>Andropogon</i> spp.										
<i>Andropogon cirratus</i>										
<i>Andropogon gerardi</i>									<1 14	
<i>Andropogon scoparius</i>										
<i>Aristida</i> spp.									<1 14	
<i>Aristida arizonica</i>										
<i>Aristida fendleriana</i>										
<i>Blepharoneuron tricholepis</i>			<1 56	<1 38	<1 11	<1 10	3 100	<1 22	1 71	<1 29
<i>Bouteloua curtipendula</i>										
<i>Bouteloua gracilis</i>									<1 14	
<i>Bromus anomalus</i>			<1 11		<1 4	<1 10				
<i>Bromus carinatus</i>										
<i>Bromus ciliatus</i>		100	2 56	100	1 59	<1 50		1 56	<1 29	
<i>Bromus frondosus</i>	<1 100	<1 100		27 100	<1 20	<1 20		<1 11		
<i>Bromus lanatipes</i>										
<i>Bromus</i> spp.			<1 11		2 30	<1 40	<1 50	<1 44	<1 14	<1 14
<i>Calamagrostis canadensis</i>										
<i>Carex</i> spp.	<1 100		1 78	<1 75	<1 63	<1 50	1 100	<1 67	<1 57	<1 100
<i>Carex foenea</i>			<1 22	2 38		<1 10		<1 14	<1 14	
<i>Carex lanuginosa</i>										
<i>Carex microptera</i>										

(Continued)

Table 5.—(continued).

HTs:	PSME/ ARUV	PSME/ HODU	PSME/ FEAR	PSME/ BRCI	PSME/ QUGA Typic ph. (27)	PSME/ QUGA MUVI ph. (10)	PSME/ QUGA FEAR ph. (2)	PSME/ MUVI	PSME/ MUMO	PSME/ QUHY
No. plots:	(2) D/C CON	(1) D/C CON	(9) D/C CON	(8) D/C CON	D/C CON	D/C CON	D/C CON	(9) D/C CON	(7) D/C CON	(7) D/C CON
<i>Aquilegia triternata</i>					<1	7				
<i>Arabis</i> spp.					<1	15			<1	29
<i>Arenaria lanuginosa</i>				<1	25				<1	14
<i>Arenaria</i> spp.										
<i>Artemisia carruthii</i>			<1	22						
<i>Artemisia dracunculoides</i>			<1	11		<1	30		<1	14
<i>Artemisia franserioides</i>			<1	11		<1	4			
<i>Artemisia franserioides</i>			<1	11		<1	7		<1	43
<i>Artemisia frigida</i>							10			
<i>Artemisia ludoviciana</i>			<1	33		<1	50		<1	14
<i>Asclepias</i> spp.										
<i>Aster falcatus</i>										
<i>Astragalus egglestonii</i>										
<i>Astragalus gilensis</i>					<1	7			<1	14
<i>Astragalus humistratus</i>										
<i>Astragalus</i> spp.			<1	11		<1	20		<1	14
<i>Bahia dissecta</i>					<1	11				
<i>Brickellia brachyphylla</i>					<1	4				
<i>Brickellia fendleri</i>										
<i>Brickellia grandiflora</i>					<1	15				
<i>Brickellia</i> spp.					<1	48				
<i>Calypso bulbosa</i>			<1	11						
<i>Campanula rotundifolia</i>			<1	11						
<i>Cardamine cordifolia</i>					<1	7			<1	57
<i>Castilleja</i> spp.			<1	11						
<i>Chaptalia aisophila</i>			<1	11		26				
<i>Chamerion angustifolium</i>			<1	11		15				
<i>Cicuta douglasii</i>										
<i>Circaea alpina</i>			<1	33						
<i>Cirsium</i> spp.					<1	11			<1	44
<i>Cirsium parryi</i>										
<i>Cirsium wheeleri</i>										
<i>Clematis ligusticifolia</i>					<1	4				
<i>Clematis pseudoalpina</i>					<1	15				
<i>Cologania longifolia</i>	<1	100		<1	25					
<i>Commelina dianthifolia</i>					<1	7			<1	14
<i>Corallorhiza</i> spp.					<1	4				
<i>Corallorhiza maculata</i>			<1	11					<1	14
<i>Cryptantha jamesii</i>					<1	4				
<i>Cucurbita foetissima</i>					<1	4				
<i>Cystopteris fragilis</i>										
<i>Delphinium tenuisectum</i>										
<i>Desmanthus cooleyi</i>					<1	25				
<i>Disporum trachycarpum</i>										

(Continued)

Table 5.—(continued).

HTs:	PSME/ ARUV	PSME/ HODU	PSME/ FEAR	PSME/ BRCI	PSME/ QUGA Typic ph. (27)	PSME/ QUGA MUVI ph. (10)	PSME/ QUGA FEAR ph. (2)	PSME/ MUVI	PSME/ MUMO	PSME/ QUHY
No. plots:.....(2)	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
<i>Carex occidentalis</i>			<1	4					<1	29
<i>Carex rossii</i>			<1	11		1	30	<1	22	29
<i>Cyperus rusbyi</i>						<1	10			
<i>Cyperus</i> sp.										
<i>Elymus glaucus</i>										
<i>Festuca arizonica</i>			10	100	<1	4	<1	10	5	100
<i>Festuca sororia</i>				<1	13					
<i>Glyceria elata</i>										
<i>Glyceria striata</i>										
<i>Koeleria nitida</i>			1	89	<1	75	1	70	<1	100
<i>Luzula parviflora</i>										
<i>Lycurus phleoides</i>										
<i>Melica porteri</i>										
<i>Muhlenbergia longiligula</i>										
<i>Muhlenbergia montana</i>	2	100	5	89	1	25	<1	37	<1	20
<i>Muhlenbergia monticola</i>										
<i>Muhlenbergia pauciflora</i>										
<i>Muhlenbergia rigens</i>										
<i>Muhlenbergia virescens</i>			<1	22						
<i>Muhlenbergia wrightii</i>										
<i>Panicum bulbosum</i>										
<i>Piptochaetium fimbriatum</i>										
<i>Poa compressa</i>										
<i>Poa fendleriana</i>			<1	67	10	88	3	96	2	60
<i>Poa nervosa</i> var <i>tracyi</i>										
<i>Poa pratensis</i>			<1	11	<1	13				
<i>Sitanion hystrix</i>			<1	67	<1	50	<1	44	1	40
<i>Sporobolus cryptandrus</i>	<1	100								
<i>Stipa</i> spp.										
<i>Stipa pringlei</i>										
<i>Trisetum montanum</i>										
Forbs										
<i>Achillea millefolium</i>										
<i>Actaea rubra</i> ssp. <i>arguta</i>	<1	50	<1	78	2	75	<1	63	1	60
<i>Agrimonia striata</i>										
<i>Allium cernuum</i>	<1	50	<1	22	<1	13	<1	22		
<i>Allium kunthii</i>										
<i>Allium rhizomatum</i>										
<i>Antennaria marginata</i>			<1	11						
<i>Antennaria parvifolia</i>			<1	22	<1	25	<1	19	<1	10
<i>Antennaria</i> spp.										
<i>Aquilegia chrysantha</i>										
<i>Aquilegia elegantula</i>										

(Continued)

Table 5.—(continued).

HTS:	PSME/ ARUV	PSME/ HODU	PSME/ FEAR	PSME/ BRCI	PSME/ QUGA Typic ph. (27)	PSME/ MUVI ph. (10)	PSME/ QUGA FEAR ph. (2)	PSME/ MUVI	PSME/ MUMO	PSME/ QUHY
No. plots:	(2) D/C CON	(1) D/C CON	(9) D/C CON	(8) D/C CON	D/C CON	D/C CON	D/C CON	(9) D/C CON	(7) D/C CON	(7) D/C CON
<i>Draba helleriana</i>			<1	33	<1	33				
<i>Dugaldia hoopesii</i>			<1	50	<1	25				
<i>Equisetum arvense</i>										
<i>Equisetum laevigatum</i>										
<i>Erigeron concinnus</i>										
<i>Erigeron delphinifolius</i>										
<i>Erigeron divergens</i>										
<i>Erigeron eximius</i>										
<i>Erigeron flagellaris</i>										
<i>Erigeron formosissimus</i>										
<i>Erigeron platyphyllus</i>										
<i>Eriogonum alatum</i>										
<i>Eriogonum jamesii</i>										
<i>Erysimum capitatum</i>										
<i>Fragaria americana</i>										
<i>Fragaria ovalis</i>										
<i>Galium</i> spp.										
<i>Galium fendleri</i>										
<i>Galium mexicanum</i>										
<i>Gaura hexandra</i>										
<i>Gentianella amarella</i> s. <i>acuta</i>										
<i>Geranium caespitosum</i>										
<i>Geranium richardsonii</i>										
<i>Geranium</i> spp.										
<i>Geum aleppicum</i> ssp. <i>strictum</i>										
<i>Gnaphalium macounii</i>										
<i>Goodyera oblongifolia</i>										
<i>Goodyera repens</i>										
<i>Halenia recurva</i>										
<i>Haplopappus parryi</i>										
<i>Hedeoma oblongifolium</i>										
<i>Hedyotis pygmaea</i>										
<i>Helianthella parryi</i>										
<i>Heterotheca fulcrata</i>										
<i>Hieracium fendleri</i>										
<i>Hydrophyllum fendleri</i>										
<i>Hymenopappus filifolius</i>										
<i>Hymenopappus mexicanus</i>										
<i>Hypericum formosum</i>										
<i>Ipomopsis aggregata</i>										
<i>Iris missouriensis</i>										
<i>Kuhnia chlorolepis</i>										
<i>Lactuca graminifolia</i>										

(Continued)

Table 5.--(continued).

HTs:	PSME/ ARUV	PSME/ HODU	PSME/ FEAR	PSME/ BRCI	PSME/ QUGA Typic ph. (27)	PSME/ QUGA MUVI ph. (10)	PSME/ QUGA FEAR ph. (2)	PSME/ MUVI	PSME/ MUMO	PSME/ QUHY				
No. plots:	(2) D/C CON	(1) D/C CON	(9) D/C CON	(8) D/C CON	D/C CON	D/C CON	D/C CON	(9) D/C CON	(7) D/C CON	(7) D/C CON				
Lathyrus arizonicus			<1	56	<1	63	<1	52	<1	50	<1	33	<1	14
Lathyrus graminifolius			<1	11	<1	13	<1	15	<1	10	<1	33	<1	14
Leucelene ericoides														
Ligusticum porteri														
Linum lewisii			<1	22	<1	13	<1	11	<1	10	<1	89	<1	14
Lithospermum multiflorum	<1	100	<1	33	<1	13	<1	74	<1	80	<1	43	<1	14
Lobelia anatina														
Lotus wrightii					<1	15	<1	15	<1	14	<1	29	<1	14
Lupinus neomexicanus					<1	4	<1	4	<1	20	<1	11	<1	14
Lupinus spp.					<1	7	<1	7	<1	10	<1	22	<1	14
Malaxis ehrenbergii			<1	11	<1	4	<1	4	<1	20	<1	11	<1	14
Malaxis soulei			<1	11	<1	25	<1	4	<1	20	<1	11	<1	14
Mertensia franciscana														
Monarda menthaefolia														
Opuntia spp. (prickly pears)														
Osmorhiza depauperata			<1	11	<1	50	<1	19	<1	20	<1	78	<1	43
Oxalis metcalfei														
Oxybaphus linearis					<1	50	<1	19	<1	20	<1	78	<1	43
Oxyypolis fendleri														
Oxytropis lambertii														
Pedicularis angustifolia														
Pedicularis grayii					<1	13	<1	70	<1	20	<1	78	<1	43
Pedicularis racemosa														
Penstemon barbatus			<1	22	<1	25	<1	70	<1	20	<1	78	<1	43
Penstemon linarioides														
Penstemon oliganthus			<1	22	<1	13	<1	70	<1	20	<1	78	<1	43
Penstemon pinifolius	<1	50	<1	22	<1	13	<1	70	<1	20	<1	78	<1	43
Penstemon whippleanus	<1	50	<1	22	<1	13	<1	70	<1	20	<1	78	<1	43
Petalostemon candidum														
Polygonum sawatchensis														
Potentilla crinita														
Potentilla gracilis v pulcher														
Potentilla hippiana					<1	15	<1	15	<1	10	<1	22	<1	14
Potentilla spp.					<1	13	<1	11	<1	20	<1	22	<1	14
Potentilla thurberi					<1	7	<1	7	<1	20	<1	22	<1	14
Prunella vulgaris														
Pseudocymopterus montanus	<1	50	<1	67	<1	50	<1	52	<1	70	<1	56	<1	29
Pseudostellaria jamesiana														
Psoralea tenuiflora														
Pteridium aquilinum			<1	11	<1	25	<1	4	<1	3	<1	33	<1	14
Pterospora andromeda					<1	4	<1	4	<1	10	<1	33	<1	14
Pyrola chlorantha			<1	11	<1	4	<1	4	<1	10	<1	33	<1	14

(Continued)

Table 5.—(continued).

HTs:	PSME/ ARUV	PSME/ HODU	PSME/ FEAR	PSME/ BRCI	PSME/ QUGA Typic ph. (27)	PSME/ QUGA MUVI ph. (10)	PSME/ QUGA FEAR ph. (2)	PSME/ MUVI D/C CON	PSME/ MUMO D/C CON	PSME/ QUHY D/C CON
No. plots:	(2) D/C CON	(1) D/C CON	(9) D/C CON	(8) D/C CON	D/C CON	D/C CON	D/C CON	(9) D/C CON	(7) D/C CON	(7) D/C CON
<i>Pyrola picta</i>				<1	13			<1	22	
<i>Ranischia secunda</i>										
<i>Ratibida columnaris</i>										
<i>Rudbeckia laciniata</i>										
<i>Rumex acetosella</i>										
<i>Rumex crispus</i>										
<i>Rumex occidentalis</i>										
<i>Senecio actinella</i>				<1	13				<1	14
<i>Senecio bigelovii</i>										
<i>Senecio cardamine</i>										
<i>Senecio cynthioides</i>			<1	<1	13	<1	15	<1	<1	14
<i>Senecio eremophilus</i>	<1	50					<1	4		
<i>Senecio neomexicanus</i>			<1	<1	13	<1	48	<1	<1	43
<i>Senecio quaerens</i>										<1
<i>Senecio wootoni</i>	<1	50	2	<1	13	<1	33	<1	<1	29
<i>Sidalcea neomexicana</i>										
<i>Silene laciniata</i>										
<i>Silene scouleri</i>			<1	<1	13	<1	11	<1	<1	14
<i>Sisymbrium linearifolium</i>			<1	<1	33	<1	7	<1	<1	29
<i>Smilacina racemosa</i>						<1	22			<1
<i>Smilacina stellata</i>	<1	50		<1	25	<1	19	<1	<1	11
<i>Solidago spathulata</i> var <i>neomex</i>										
<i>Solidago</i> spp.	4	100				<1	33	<1	<1	14
<i>Solidago wrightii</i>									<1	29
<i>Sphaeralcea coccinea</i>										
<i>Swertia radiata</i>										
<i>Taraxacum</i> spp.						<1	4			
<i>Thalictrum fendleri</i>			<1	<1	50	<1	63	<1	<1	14
<i>Thermopsis pinetorum</i>				<1		<1	11	<1	<1	33
<i>Townsendia formosa</i>						<1	4			
<i>Tragia stylaris</i>										
<i>Valeriana capitata</i>				<1	38	<1	33			
<i>Valeriana edulis</i>						<1	10			
<i>Veratrum californicum</i>										
<i>Verbascum thapsus</i>			<1	11						
<i>Vicia americana</i>			<1	56	2	88	<1	52	<1	29
<i>Vicia leucophaea</i>							<1	4		
<i>Vicia puichella</i>			<1	33			<1	7	<1	43
<i>Viguiera multiflora</i>							<1	4	<1	14
<i>Viola canadensis</i>				<1	25		<1	33	<1	
<i>Viola nephrophylla</i>										
<i>Zygadenus elegans</i>				<1	25		<1	7		
<i>Zygadenus virescens</i>										

Table 6.--Tree density (D) or shrub-herb cover (C) and constancy (CON) for Apache-Gila-Cibola(Madg.):
Pinus ponderosa series.

[illegible]

PIRO/ Rockland	PIPO/FEAR Typle ph.	PIPO/FEAR QUGA ph.	PIPO/FEAR BOGR ph.	PIPO/MUMO	PIPO/QUGA Typle ph.	PIPO/QUGA MULO ph.	PIPO/BOGR PIED ph.	PIPO/BOGR VIAR ph.	PIPO/ARPU CT
(3) D/C CON	(5) D/C CON	(1) D/C CON	(7) D/C CON	(10) D/C CON	(8) D/C CON	(4) D/C CON	(11) D/C CON	(1) D/C CON	(2) D/C CON

Trees

5 33	<1 20	1 100	<1 14	6 90	1 50	3 50	5 91	7 100	
4 33			<1 14	2 70	<1 13	3 25	2 82	3 100	3 100
1 33		1 100	<1 14	<1 30	<1 13		<1 18		
			<1 14		<1 13				

	<1 20			<1 10		3 50			
				<1 10					

3 33	<1 20		2 29	1 50	5 75	11 100	2 36		1 50
2 33			<1 14	<1 30		<1 25	<1 18		
						<1 25			
2 67	2 60	2 100	2 71	8 60	3 100	5 75	2 64	22 100	6 50
3 67	7 100	4 100	4 71	5 60	5 88	11 100	2 73	4 100	14 100
2 67	5 100	1 100	4 100	3 90	5 100	6 100	3 91	4 100	2 100

2 33				<1 10	<1 38	<1 25			
1 33					<1 38	<1 25			
<1 33									

Shrubs

<1 33				<1 30	<1 13	<1 25	<1 18	<1 100	<1 50
<1 33				1 10	<1 13	<1 25	<1 9	<1 100	<1 50
<1 33				<1 20	<1 25	<1 25			10 50
					<1 13	<1 50			

(continued)

HTs:	PIPO/MUVI	PIPO/MUVI	PIPO/MUVI	PIPO/MUVI	PIPO/MUVI	PIPO/MUVI	PIPO/MUVI
No. plots:	Typeic ph. (3)	QUGA ph. (4)	Typeic ph. (11)	QUGA ph. (3)	BOGR ph (4)	MUMO ph. (7)	MULO ph. (9)
	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON	D/C CON
Garrya wrightii							< 1 22
Gutierrezia sarothrae					< 1 25		
Holodiscus dumosus							
Hymenoxys richardsonii				< 1 33	< 1 25	< 1 14	
Jamesia americana							
Juglans major							
Juniperus communis							
Lonicera albiflora							< 1 11
Lonicera arizonica							
Nolina microcarpa							< 1 11
Parthenocissus vitacea							
Philadelphus spp.							
Physocarpus monogynus							
Populus tremuloides - shrubs							
Ptelea trifoliata							
Prunus emarginata							
Prunus virginiana							
Quercus chrysolepis							
Quercus emoryi							< 1 11
Quercus gambelii	< 1 33	5 100	< 1 36	2 100		< 1 14	< 1 44
Quercus grisea	2 33	< 1 50				11 100	12 100
Quercus hypoleucoides							< 1 11
Quercus rugosa							
Rhamnus betulaeifolia							
Rhus glabra							
Rhus trilobata							< 1 22
Ribes cereum							
Ribes montigenum							
Ribes pinetorum							
Ribes wolfii							
Robinia neomexicana	< 1 33						
Rosa spp.	< 1 33		< 1 18				
Rubus arizonensis							
Rubus parviflorus							
Rubus strigosus							
Salix bebbiana							
Salix scouleriana							
Salix spp.							
Sambucus spp.			< 1 9				
Shepherdia canadensis							
Sorbus dumosa							
Symphoricarpus oreophilus	< 1 33						
Toxicodendron rydbergii							
Vaccinium myrtillus							
Vitis arizonica							
Yucca baccata						< 1 43	< 1 22
Yucca schottii							
Graminoids							
Agropyron arizonicum						< 1 14	
Agropyron (smithii?)							
Agrostis alba							
Andropogon spp.		< 1 25					
Andropogon cirratus							< 1 11
Andropogon gerardi						< 1 14	
Andropogon scoparius					< 1 25	< 1 14	

PIRO/ Rockland	PIPO/FEAR Typic ph.	PIPO/FEAR QUGA ph.	PIPO/FEAR BOGR ph.	PIPO/MUMO	PIPO/QUGA Typic ph.	PIPO/QUGA MULO ph.	PIPO/BOGR PIED ph.	PIPO/BOGR VIAR ph.	PIPO/ARPU CT
(3) D/C CON	(5) D/C CON	(1) D/C CON	(7) D/C CON	(10) D/C CON	(8) D/C CON	(4) D/C CON	(11) D/C CON	(1) D/C CON	(2) D/C CON
						< 1 25			< 1 100
< 1 33			< 1 43	< 1 10			< 1 18		
							< 1 100		
								< 1 50	
							< 1 100		
							< 1 100		
2 33	< 1 80 < 1 40	1 100	< 1 43 < 1 14	2 80 < 1 90	34 100 < 1 13 < 1 13	12 100 < 1 75 1 50	1 55 1 55 < 1 9	25 100	1 100 < 1 100 30 50
								< 1 100	
< 1 33			< 1 43			< 1 50	< 1 9		< 1 50
					< 1 38	< 1 25			
								5 100	
< 1 33				< 1 10	< 1 13	< 1 25			
Graminoids									
							< 1 9		
	< 1 40		< 1 29	2 50 1 10		2 25	1 36 < 1 9		
			2 14	< 1 10					

(continued)

Table 6.—(continued).

HTs:	PIPO/MUVI		PIPO/MUVI		PIPO/MUVI -FEAR		PIPO/MUVI -FEAR		PIPO/MUVI -FEAR		PIPO/QUGR		PIPO/QUGR	
No. plots:	Type ph. (3)		QUGA ph. (4)		Type ph. (11)		QUGA ph. (3)		BOGR ph (4)		MUMO ph. (7)		MULO ph. (9)	
	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON	D/C	CON
Aristida spp.														
Aristida arizonica											<1	43	<1	11
Aristida fendleriana														
Blepharoneuron tricholepis	1	67	<1	100	1	91	3	100	5	100	<1	86	<1	33
Bouteloua curtipendula													<1	33
Bouteloua gracilis			<1	25			<1	33	1	100	2	43	<1	56
Bromus anomalus	<1	67			<1	9								
Bromus carinatus					<1	9								
Bromus ciliatus					<1	9					<1	14		
Bromus frondosus					<1	9					<1	14		
Bromus lanatipes														
Bromus spp.			1	50	<1	73	1	100	<1	25	<1	14	<1	44
Calamagrostis canadensis														
Carex spp.	<1	67	<1	100	<1	73	<1	100	<1	75	<1	86	<1	67
Carex foenea					<1	18								
Carex lanuginosa														
Carex microptera														
Carex occidentalis														
Carex rossii														
Cyperus rusbyi	<1	33									<1	43	<1	22
Cyperus sp.											<1	14		
Elymus glaucus														
Festuca arizonica					4	100	6	100	7	100				
Festuca sororia														
Glyceria elata														
Glyceria striata														
Koeleria nitida			1	75	2	91	6	100	6	100	<1	100	<1	56
Luzula parviflora														
Lycurus phleoides											<1	43		
Melica porteri														
Muhlenbergia longiligula	<1	33									<1	14	4	100
Muhlenbergia montana	2	67	<1	50	4	55					5	100	<1	11
Muhlenbergia monticola														
Muhlenbergia pauciflora													<1	11
Muhlenbergia rigens									<1	25	<1	14	<1	33
Muhlenbergia virescens	19	100	11	100	5	91	8	100	8	100	2	57	1	22
Muhlenbergia wrightii					<1	9			<1	25				
Panicum bulbosum					<1	9								
Piptochaetium fimbriatum													<1	33
Poa compressa						<1	9							
Poa fendleriana	<1	67	<1	50	3	100	3	100	<1	50	3	71	<1	67
Poa nervosa var tracyi														
Poa pratensis					<1	9								
Sitanion hystrix	<1	33	<1	100	3	91	5	100	2	100	<1	100	<1	78
Sporobolus cryptandrus														
Stipa spp.														
Stipa pringlei					<1	18	<1	33	<1	25				
Trisetum montanum														
Forbs														
Achillea millefolium	<1	33			2	82					<1	29		
Actaea rubra ssp. arguta														
Agrimonia striata														
Allium cernuum					<1	9					<1	14		
Allium kunthii														
Allium rhizomatum														

PIRO/ Rockland	PIPO/FEAR Typic ph.	PIPO/FEAR QUGA ph.	PIPO/FEAR BOGR ph.	PIPO/MUMO	PIPO/QUGA Typic ph.	PIPO/QUGA MULO ph.	PIPO/BOGR PIED ph.	PIPO/BOGR VIAR ph.	PIPO/ARPU CT
(3) D/C CON	(5) D/C CON	(1) D/C CON	(7) D/C CON	(10) D/C CON	(8) D/C CON	(4) D/C CON	(11) D/C CON	(1) D/C CON	(2) D/C CON
	<1 80		<1 57	<1 60		<1 25	<1 9 2 82 <1 9	<1 100 3 100	
<1 33 <1 33 1 33 <1 33	3 80 <1 20	4 100	3 71 6 100	2 100 <1 10 2 100	<1 38 <1 25	<1 25 <1 25 <1 50	<1 64 <1 9 18 100 <1 18	25 100	
				<1 10 <1 10 <1 10	<1 13		<1 18	<1 100	
	<1 40			<1 30	<1 50	<1 25	<1 27	<1 100	
<1 33	<1 40		1 71	<1 70	<1 63	1 100	<1 73		<1 50
<1 33	<1 20			<1 20			<1 9	<1 100	
<1 33	3 100	2 100	7 100		<1 13				
<1 33	<1 100	<1 100	3 57 <1 29	<1 90 <1 20	<1 63	<1 50	1 55 <1 55	<1 100	
<1 33 4 67	16 100	8 100	7 86	<1 10 10 100	<1 13 <1 50	5 100	<1 9 <1 36		<1 50
<1 33 1 33	<1 40		<1 14 <1 14	<1 40 <1 10 <1 10	<1 38	<1 25	<1 18 <1 18		<1 50
				<1 20			<1 9	<1 100	
<1 33	<1 40	4 100	1 86	2 60	3 100	<1 100	<1 64		<1 50
	1 80 13 20	3 100	3 100	3 100	2 88	<1 50	<1 9 2 100 <1 9	<1 100	<1 50 <1 50
Forbs <1 33	<1 40	3 100	<1 29	<1 40	<1 63	<1 25	<1 18 <1 9		
	<1 40		<1 14	1 30					

(continued)

Table 6.--(continued).[illegible]

PIPO/ Rockland	PIPO/FEAR Typic ph.	PIPO/FEAR QUGA ph.	PIPO/FEAR BOGR ph.	PIPO/MUMO	PIPO/QUGA Typic ph.	PIPO/QUGA MULO ph.	PIPO/BOGR PIED ph.	PIPO/BOGR VIAR ph.	PIPO/ARPU CT
(3) D/C CON	(5) D/C CON	(1) D/C CON	(7) D/C CON	(10) D/C CON	(8) D/C CON	(4) D/C CON	(11) D/C CON	(1) D/C CON	(2) D/C CON
<1 33	<1 40			<1 10 <1 20	<1 25	<1 25			
			<1 29		<1 13	<1 50	<1 18	<1 100	
1 33			<1 14	<1 30	<1 13 1 88	<1 75	<1 27		<1 100
<1 67	<1 80		<1 29 <1 29	<1 30	<1 13	<1 50	<1 9 <1 45	8 100	
	<1 20		<1 14 <1 14	<1 20 <1 10	<1 13 <1 13		<1 9 <1 36		
	<1 60	<1 100	<1 29	<1 20	<1 25	<1 50	<1 18 <1 27		
	<1 40 <1 20	<1 100	<1 43	<1 20 <1 30	<1 13 <1 25		<1 64		
<1 67				<1 10	<1 50	<1 25			<1 50
<1 33									
<1 33	<1 40		<1 86	<1 20	<1 25	<1 25	<1 45		
	<1 20		<1 14	<1 10					
<1 33 <1 33	<1 20			<1 30 <1 30	<1 13		<1 18 <1 9		
	<1 20		<1 43	<1 10			<1 18 <1 9		
					<1 13				
<1 33	<1 20				<1 13		<1 18		
<1 33	<1 20	1 100		<1 10 <1 20	<1 13	<1 25	<1 18		

(continued)

Table 6.--(continued).

HTs:	PIPO/MUVI		PIPO/MUVI		PIPO/MUVI -FEAR		PIPO/MUVI -FEAR		PIPO/MUVI -FEAR		PIPO/QUGR		PIPO/QUGR	
No. plots:	Typic (3)	ph. D/C CON	QUGA (4)	ph. D/C CON	Typic (11)	ph. D/C CON	QUGA (3)	ph. D/C CON	BOGR (4)	ph. D/C CON	MUMO (7)	ph. D/C CON	MULO (9)	ph. D/C CON
<i>Erigeron flagellaris</i>	<1	100	<1	25	<1	45	<1	67	<1	50	<1	43	<1	33
<i>Erigeron formosissimus</i>			<1	25	<1	9					<1	14		
<i>Erigeron platyphyllus</i>	<1	33	<1	50	<1	36			<1	25	<1	14	<1	11
<i>Eriogonum alatum</i>			<1	25	<1	18	<1	67	<1	75	<1	43	<1	44
<i>Eriogonum jamesii</i>	<1	33							<1	50	<1	43		
<i>Erysimum capitatum</i>	<1	33									<1	14		
<i>Fragaria americana</i>														
<i>Fragaria ovalis</i>	<1	33			<1	9								
<i>Galium</i> spp.					<1	9	<1	33			<1	14		
<i>Galium fendleri</i>														
<i>Galium mexicanum</i>														
<i>Gaura hexandra</i>			<1	25							<1	14	<1	11
<i>Gentianella amarella</i> s. <i>acuta</i>					<1	9								
<i>Geranium caespitosum</i>	<1	67	<1	75	<1	82	<1	33	<1	50	<1	57	<1	56
<i>Geranium richardsonii</i>														
<i>Geranium</i> spp.	<1	33					<1	33						
<i>Geum aleppicum</i> ssp. <i>strictum</i>														
<i>Gnaphalium macounii</i>														
<i>Goodyera oblongifolia</i>														
<i>Goodyera repens</i>														
<i>Halenia recurva</i>					<1	18								
<i>Haplopappus parryi</i>					<1	9								
<i>Hedeoma oblongifolium</i>	<1	33	<1	25							<1	29	<1	44
<i>Hedyotis pygmaea</i>			<1	25	<1	36					<1	43	<1	33
<i>Helianthella parryi</i>			<1	25							<1	14		
<i>Heterotheca fulcrata</i>			<1	25	<1	18	<1	67	<1	25				
<i>Hieracium fendleri</i>			<1	25	<1	36	<1	33			<1	14	<1	33
<i>Hydrophyllum fendleri</i>														
<i>Hymenopappus filifolius</i>														
<i>Hymenopappus mexicanus</i>			<1	50	<1	9	<1	33					<1	11
<i>Hypericum formosum</i>														
<i>Ipomopsis aggregata</i>	<1	33	<1	100	<1	36	<1	67			<1	43	<1	22
<i>Iris missouriensis</i>	<1	33			<1	18			<1	25	<1	29	<1	33
<i>Kuhnia chlorolepis</i>									<1	25				
<i>Lactuca graminifolia</i>														
<i>Lathyrus arizonicus</i>	<1	33			<1	18			<1	25	<1	14		
<i>Lathyrus graminifolius</i>	<1	33	<1	25	<1	27	<1	33			<1	14		
<i>Leucelene ericoides</i>														
<i>Ligusticum porteri</i>														
<i>Linum lewisii</i>	<1	33			<1	9					<1	14		
<i>Lithospermum multiflorum</i>	<1	33	<1	75	<1	45	<1	100	<1	25	<1	29	<1	44
<i>Lobelia anatina</i>					<1	9								
<i>Lotus wrightii</i>	<1	67	<1	50	<1	27	<1	33	<1	50	<1	43	<1	44
<i>Lupinus neomexicanus</i>					1	9							<1	11
<i>Lupinus</i> spp.	<1	33												
<i>Malaxis ehrenbergii</i>														
<i>Malaxis soulei</i>	<1	33												
<i>Mertensia franciscana</i>														
<i>Monarda menthaefolia</i>														
<i>Opuntia</i> spp. (prickly pears)											<1	14	<1	33
<i>Osmorhiza depauperata</i>														
<i>Oxalis metcalfei</i>					<1	9								
<i>Oxybaphus linearis</i>											<1	29		
<i>Oxytropis fendleri</i>														
<i>Oxytropis lambertii</i>			<1	25	<1	9	<1	33	<1	50	<1	14	<1	11
<i>Pedicularis angustifolia</i>														

PIRO/ Rockland	PIPO/FEAR Typic ph.	PIPO/FEAR QUGA ph.	PIPO/FEAR BOGR ph.	PIPO/MUMO	PIPO/QUGA Typic ph.	PIPO/QUGA MULO ph.	PIPO/BOGR PIED ph.	PIPO/BOGR VIAR ph.	PIPO/ARPU CT
(3) D/C CON	(5) D/C CON	(1) D/C CON	(7) D/C CON	(10) D/C CON	(8) D/C CON	(4) D/C CON	(11) D/C CON	(1) D/C CON	(2) D/C CON
1 33	<1 40	4 100	<1 57	<1 40	<1 38	<1 75	2 82		<1 50
<1 67	<1 60			<1 20					
<1 67	<1 20		<1 43	<1 10	<1 25	<1 25			
<1 33	<1 20			<1 40	<1 13	<1 25	<1 64		
			<1 14		<1 25		<1 9		
	<1 20								
				<1 10					
<1 33						<1 25			<1 50
					<1 13				
	<1 40	<1 100					<1 9		
<1 100	<1 40	1 100	<1 43	<1 60	<1 88	<1 25	1 91	<1 100	<1 50
<1 33									
<1 33	<1 60	<1 100	<1 29	<1 60			<1 64		
	<1 20								
<1 33							<1 18		
<1 67	<1 20	<1 100	<1 57	<1 30	<1 13	<1 25	<1 9		
						<1 25			
<1 67	<1 40						<1 18		
<1 33	<1 40		<1 29	<1 20	<1 63	<1 25	<1 27		
<1 33								<1 100	
					<1 13				
<1 33	<1 20	<1 100	<1 29	<1 30	<1 50	<1 25			
	<1 20		<1 29	<1 10			<1 9		
<1 33	<1 20		<1 14	<1 10			<1 9		
<1 67	<1 40		<1 14	<1 20	<1 88	<1 50			
				<1 10					
<1 33	<1 20		<1 14	<1 70	<1 50	<1 100	<1 91	<1 100	
	<1 20								
					<1 13			<1 100	
<1 33				<1 20		<1 25	<1 18		
<1 33			<1 14				<1 18		
<1 33				<1 10					
	<1 40	<1 100	<1 43				<1 9		

(continued)

[illegible]

PIRO/ Rockland	PIPO/FEAR Typic ph.	PIPO/FEAR QUGA ph.	PIPO/FEAR BOGR ph.	PIPO/MUMO	PIPO/QUGA Typic ph.	PIPO/QUGA MULO ph.	PIPO/BOGR PIED ph.	PIPO/BOGR VIAR ph.	PIPO/ARPU CT
(3) D/C CON	(5) D/C CON	(1) D/C CON	(7) D/C CON	(10) D/C CON	(8) D/C CON	(4) D/C CON	(11) D/C CON	(1) D/C CON	(2) D/C CON
<1 33			<1 14		<1 25	<1 25	<1 9 <1 9	<1 100	
<1 33			<1 14 <1 14 <1 14	<1 10 <1 10		<1 50	<1 27 <1 18 <1 9		
<1 33	<1 20 <1 40 <1 20	<1 100	<1 14	<1 10				<1 100	
	<1 80		<1 57	<1 60	<1 38 <1 13	<1 25	<1 36		
							<1 9		
	<1 40			<1 10			<1 36		
<1 100 <1 33	<1 60		<1 14	<1 60	<1 63 <1 13 <1 20	<1 75	<1 45	<1 100	<1 50
			<1 14	<1 10 <1 20	<1 38	<1 25	<1 36		
				<1 20	<1 25	<1 75	<1 9		
		<1 100	<1 14	<1 20 <1 10			<1 55 <1 18	<1 100	
				<1 30	<1 63 <1 13		<1 9		
<1 33 <1 33					<1 13		<1 9 <1 9		
			<1 29				<1 9		

(continued)

Table 6.--(continued).[illegible]

PIRO/ Rockland	PIPO/FEAR Typic ph.	PIPO/FEAR QUGA ph.	PIPO/FEAR BOGR ph.	PIPO/MUMO	PIPO/QUGA Typic ph.	PIPO/QUGA MULO ph.	PIPO/BOGR PIED ph.	PIPO/BOGR VIAR ph.	PIPO/ARPU CT
(3) D/C CON	(5) D/C CON	(1) D/C CON	(7) D/C CON	(10) D/C CON	(8) D/C CON	(4) D/C CON	(11) D/C CON	(1) D/C CON	(2) D/C CON
	<1 20			<1 10	<1 25		<1 9		
	<1 20			<1 10		<1 25	<1 18		
<1 67			<1 14	<1 10	<1 25		<1 9		
<1 33	<1 20			<1 20	<1 25	<1 25	<1 27		

**Table 7.--Tree density (D) or shrub-herb cover (C) and constancy (CON) for Apache-Gila-Cibola(Madg.):
Populus angustifolia series.**

HTs: POAN			HTs: POAN		
No. plots: (9)			No. plots: (9)		
	D/C	CON		D/C	CON
Trees					
Abies concolor - Young regen.	8	44	Alnus oblongifolia	16	44
Abies concolor - Advance regen.	4	44	Berberis repens		
Abies concolor - Mature	< 1	22	Calliandra humilis		
Abies lasiocarpa - Young regen.			Ceanothus fendleri		
Abies lasiocarpa - Advance regen.			Cercocarpus montanus		
Abies lasiocarpa - Mature			Chimaphila umbellata	< 1	11
Alnus oblongifolia - Young regen.	1	11	Cornus stolonifera	< 1	11
Alnus oblongifolia - Advance regen.	1	33	Fraxinus pennsylvanica	< 1	22
Alnus oblongifolia - Mature	< 1	44	Garrya wrightii		
Juniperus deppeana - Young regen.	< 1	22	Gutierrezia sarothrae		
Juniperus deppeana - Advance regen.	< 1	22	Holodiscus dumosus	< 1	11
Juniperus deppeana - Mature			Hymenoxys richardsonii		
Juniperus osteosperma - Young regen.			Jamesia americana	< 1	11
Juniperus osteosperma - Advance regen.			Juglans major	3	44
Juniperus osteosperma - Mature			Juniperus communis		
Juniperus scopulorum - Young regen.	< 1	11	Lonicera albiflora		
Juniperus scopulorum - Advance regen.			Lonicera arizonica	< 1	11
Juniperus scopulorum - Mature			Nolina microcarpa		
Picea engelmannii - Young regen.			Parthenocissus vitacea	2	33
Picea engelmannii - Advance regen.			Philadelphus spp.		
Picea engelmannii - Mature			Physocarpus monogynus	< 1	11
Picea pungens - Young regen.			Populus tremuloides - shrubs		
Picea pungens - Advance regen.			Ptelea trifoliata	< 1	22
Picea pungens - Mature			Prunus emarginata		
Pinus edulis - Young regen.	< 1	11	Prunus virginiana	< 1	11
Pinus edulis - Advance regen.			Quercus chrysolepis		
Pinus edulis - Mature			Quercus emoryi		
Pinus ponderosa - Young regen.	< 1	11	Quercus gambelii	6	67
Pinus ponderosa - Advance regen.	1	44	Quercus grisea		
Pinus ponderosa - Mature	1	44	Quercus hypoleucoides	< 1	11
Pinus strobiformis - Young regen.	< 1	22	Quercus rugosa	2	22
Pinus strobiformis - Advance regen.			Rhamnus betulaefolia	1	44
Pinus strobiformis - Mature	< 1	22	Rhus glabra	2	11
Populus angustifolia - Young regen.	1	22	Rhus trilobata	< 1	11
Populus angustifolia - Advance regen.	2	33	Ribes cereum		
Populus angustifolia - Mature	< 1	33	Ribes montigenum		
Populus tremuloides - Young regen.			Ribes pinetorum		
Populus tremuloides - Advance regen.			Ribes wolfii		
Populus tremuloides - Mature			Robinia neomexicana	< 1	11
Pseudotsuga menziesii - Young regen.	3	67	Rosa spp.	< 1	11
Pseudotsuga menziesii - Advance regen.	4	56	Rubus arizonensis	< 1	11
Pseudotsuga menziesii - Mature	< 1	44	Rubus parviflorus		
			Rubus strigosus	< 1	11
			Salix bebbiana		
			Salix scouleriana		
			Salix spp.	3	44
Shrubs					
Acer glabrum	< 1	22			
Acer grandidentatum	2	11			
Acer negundo	3	33			

(continued)

Table 7.--(continued).

HTs: POAN			HTs: POAN		
No. plots: (9)			No. plots: (9)		
	D/C	CON		D/C	CON
<i>Sambucus</i> spp.			<i>Muhlenbergia longiligula</i>		
<i>Shepherdia canadensis</i>			<i>Muhlenbergia montana</i>	< 1	11
<i>Sorbus dumosa</i>			<i>Muhlenbergia monticola</i>		
<i>Symphoricarpus oreophilus</i>	< 1	22	<i>Muhlenbergia pauciflora</i>		
<i>Toxicodendron rydbergii</i>	< 1	44	<i>Muhlenbergia rigens</i>	< 1	11
<i>Vaccinium myrtillus</i>			<i>Muhlenbergia virescens</i>	< 1	22
<i>Vitis arizonica</i>	1	44	<i>Muhlenbergia wrightii</i>	< 1	11
<i>Yucca baccata</i>			<i>Panicum bulbosum</i>		
<i>Yucca schottii</i>			<i>Piptochaetium fimbriatum</i>		
Graminoids			<i>Poa compressa</i>	< 1	11
<i>Agropyron arizonicum</i>			<i>Poa fendleriana</i>	2	67
<i>Agropyron (smithii?)</i>	1	11	<i>Poa nervosa</i> var <i>tracyi</i>		
<i>Agrostis alba</i>	< 1	11	<i>Poa pratensis</i>	8	56
<i>Andropogon</i> spp.			<i>Sitanion hystrix</i>	< 1	33
<i>Andropogon cirratus</i>			<i>Sporobolus cryptandrus</i>		
<i>Andropogon gerardi</i>			<i>Stipa</i> spp.		
<i>Andropogon scoparius</i>			<i>Stipa pringlei</i>	< 1	11
<i>Aristida</i> spp.			<i>Trisetum montanum</i>		
<i>Aristida arizonica</i>	< 1	11	Forbs		
<i>Aristida fendleriana</i>			<i>Achillea millefolium</i>	< 1	33
<i>Blepharoneuron tricholepis</i>	< 1	22	<i>Actaea rubra</i> ssp. <i>arguta</i>	< 1	11
<i>Bouteloua curtipendula</i>			<i>Agrimonia striata</i>	1	33
<i>Bouteloua gracilis</i>	< 1	11	<i>Allium cernuum</i>		
<i>Bromus anomalus</i>			<i>Allium kunthii</i>		
<i>Bromus carinatus</i>			<i>Allium rhizomatum</i>		
<i>Bromus ciliatus</i>	< 1	33	<i>Antennaria marginata</i>		
<i>Bromus frondosus</i>			<i>Antennaria parvifolia</i>		
<i>Bromus lanatipes</i>	< 1	33	<i>Antennaria</i> spp.		
<i>Bromus</i> spp.	2	33	<i>Aquilegia chrysantha</i>	< 1	22
<i>Calamagrostis canadensis</i>			<i>Aquilegia elegantula</i>		
<i>Carex</i> spp.	< 1	67	<i>Aquilegia triterata</i>		
<i>Carex foenea</i>			<i>Arabis</i> spp.	< 1	11
<i>Carex lanuginosa</i>			<i>Arenaria lanuginosa</i>		
<i>Carex microptera</i>			<i>Arenaria</i> spp.		
<i>Carex occidentalis</i>	< 1	33	<i>Artemisia carruthii</i>	< 1	33
<i>Carex rossii</i>	< 1	11	<i>Artemisia dracunculoides</i>	< 1	11
<i>Cyperus rusbyi</i>			<i>Artemisia franserioides</i>		
<i>Cyperus</i> sp.			<i>Artemisia frigida</i>		
<i>Elymus glaucus</i>			<i>Artemisia ludoviciana</i>	< 1	33
<i>Festuca arizonica</i>			<i>Asclepias</i> spp.	< 1	11
<i>Festuca sororia</i>			<i>Aster falcatus</i>		
<i>Glyceria elata</i>	< 1	11	<i>Astragalus egglestonii</i>		
<i>Glyceria striata</i>	< 1	11	<i>Astragalus gilensis</i>		
<i>Koeleria nitida</i>			<i>Astragalus humistratus</i>		
<i>Luzula parviflora</i>			<i>Astragalus</i> spp.		
<i>Lycurus phleoides</i>			<i>Bahia dissecta</i>	< 1	11
<i>Melica porteri</i>	< 1	11			

(continued)

Table 7.--(continued).

HTs: POAN			HTs: POAN		
No. plots: (9)			No. plots: (9)		
	D/C	CON		D/C	CON
Brickellia brachyphylla			Gentianella amarella s. acuta		
Brickellia fendleri			Geranium caespitosum	< 1	33
Brickellia grandiflora			Geranium richarsonii	< 1	22
Brickellia spp.	< 1	56	Geranium spp.	< 1	22
Calypso bulbosa			Geum aleppicum ssp. strictum		
Campanula rotundifolia	< 1	11	Gnaphalium macounii		
Cardamine cordifolia	< 1	11	Goodyera oblongifolia		
Castilleja spp.			Goodyera repens		
Chaptalia alsophila			Halenia recurva		
Chamerlon angustifolium			Haplopappus parryi		
Cicuta douglasii	< 1	11	Hedeoma oblongifolium		
Circaea alpina	1	22	Hedyotis pygmaea		
Cirsium spp.			Helianthella parryi		
Cirsium parryi			Heterotheca fulcrata	< 1	11
Cirsium wheeleri			Hieracium fendleri		
Clematis ligusticifolia	< 1	33	Hydrophyllum fendleri		
Clematis pseudoalpina			Hymenopappus filifolius		
Cologania longifolia			Hymenopappus mexicanus	< 1	11
Commelina dianthifolia			Hypericum formosum	< 1	11
Corallorhiza spp.			Ipomopsis aggregata	< 1	22
Corallorhiza maculata	< 1	11	Iris missouriensis		
Cryptantha jamesii			Kuhnia chlorolepis		
Cucurbita foetidissima			Lactuca graminifolia	< 1	22
Cystopteris fragilis	< 1	22	Lathyrus arizonicus	< 1	56
Delphinium tenuisectum			Lathyrus graminifolius	< 1	11
Desmanthus cooleyi			Leucelene ericoides		
Disporum trachycarpum			Ligusticum porteri	< 1	22
Draba helleriana	< 1	11	Linum lewisii		
Dugaldia hoopesii			Lithospermum multiflorum	< 1	11
Equisetum arvense	< 1	11	Lobelia anatina		
Equisetum laevigatum	< 1	11	Lotus wrightii		
Erigeron concinnus			Lupinus neomexicanus	< 1	11
Erigeron delphinifolius			Lupinus spp.		
Erigeron divergens			Malaxis ehrenbergii		
Erigeron eximius			Malaxis soulei		
Erigeron flagellaris	< 1	11	Mertensia franciscana	< 1	11
Erigeron formosissimus			Monarda menthaefolia	4	67
Erigeron platyphyllus			Opuntia spp. (prickly pears)		
Eriogonum alatum			Osmorhiza depauperata	< 1	11
Eriogonum jamesii			Oxalis metcalfei	< 1	11
Erysimum capitatum			Oxybaphus linearis		
Fragaria americana	< 1	11	Oxytropis fendleri	< 1	11
Fragaria ovalis	< 1	11	Oxytropis lambertii		
Galium spp.			Pedicularis angustifolia		
Galium fendleri			Pedicularis grayii		
Galium mexicanum	< 1	11	Pedicularis racemosa		
Gaura hexandra	< 1	11			

(continued)

Table 7.--(continued).

HTs: POAN			HTs: POAN		
No. plots: (9)			No. plots: (9)		
	D/C	CON		D/C	CON
Penstemon barbatus	< 1	22	Senecio neomexicanus	< 1	11
Penstemon linarioides			Senecio quaerens	2	56
Penstemon oliganthus			Senecio wootoni	< 1	22
Penstemon pinifolius			Sidalcea neomexicana		
Penstemon whippleanus			Silene laciniata		
Petalostemon candidum			Silene scouleri		
Polygonum sawatchensis			Sisymbrium linearifolium		
Potentilla crinita			Smilacina racemosa	< 1	33
Potentilla gracilis v pulcher			Smilacina stellata	< 1	11
Potentilla hippiana			Solidago spathulata var neomex		
Potentilla spp.			Solidago spp.	< 1	22
Potentilla thurberi			Solidago wrightii		
Prunella vulgaris	< 1	22	Sphaeralcea coccinea		
Pseudocymopterus montanus	< 1	11	Swertia radiata	< 1	11
Pseudostellaria jamesiana			Taraxacum spp.	2	44
Psoralea tenuiflora			Thalictrum fendleri	1	67
Pteridium aquilinum			Thermopsis pinetorum		
Pterospora andromeda			Townsendia formosa		
Pyrola chlorantha	< 1	11	Tragla stylaris		
Pyrola picta	< 1	11	Valeriana capitata	< 1	22
Ramischia secunda			Valeriana edulis		
Ratibida columnaris			Veratrum californicum	< 1	11
Rudbeckia laciniata	< 1	11	Verbascum thapsus	< 1	33
Rumex acetosella	< 1	22	Vicia americana	< 1	33
Rumex crispus			Vicia leucophaea		
Rumex occidentalis			Vicia pulchella	< 1	22
Senecio actinella			Viguiera multiflora	< 1	11
Senecio bigelovii			Viola canadensis	< 1	56
Senecio cardamine			Viola nephrophylla	< 1	11
Senecio cynthioides			Zygadenus elegans		
Senecio eremophilus			Zygadenus virescens		

Appendix E. Plants indicative of riparian sites. (The list includes some species that are associated with streamside zones according to the Riparian Area Handbook¹⁵, but not others that sometimes may be found in nonriparian situations as well.)

Trees

Acer grandidentatum
Acer negundo
Alnus oblongifolia
Juglans major

Shrubs and Vines

Cornus stolonifera
Potentilla fruticosa
Salix bebbiana
Salix subcoerulea
Vitis arizonica

Graminoids

Glyceria spp.
Juncus spp.
Scirpus microcarpus

Forbs

Aconitum columbianum
Cicuta douglasii
Equisetum spp.
Prunella vulgaris
Ranunculus hydrocharioides
Rudbeckia laciniata
Veratrum californicum

¹⁵Riparian Area Handbook. Forest Service Handbook 2509.23, U.S. Forest Service, Southwestern Region, Albuquerque, New Mexico, February 1985.





Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526



United States
Department of
Agriculture

Forest Service

**Rocky Mountain
Forest and Range
Experiment Station**

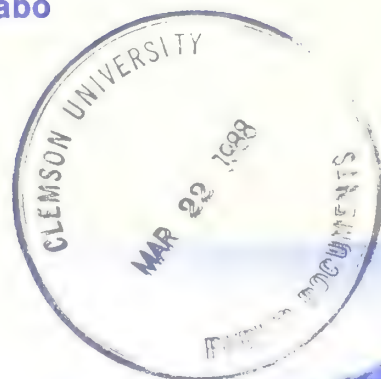
Fort Collins,
Colorado 80526

**General Technical
Report RM-146**



Guidelines for Measuring the Physical, Chemical, and Biological Condition of Wilderness Ecosystems

**Douglas G. Fox
J. Christopher Bernabo
Betsy Hood**



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Guidelines include a large number of specific measures to characterize the existing condition of wilderness resources. Measures involve the atmospheric environment, water chemistry and biology, geology and soils, and flora. Where possible, measures are coordinated with existing long-term monitoring programs. Application of the measures will allow more effective evaluation of proposed new air pollution sources.

Keywords: Monitoring, Wilderness, Baseline Conditions, Air Pollution,
Atmospheric Deposition

The use of trade and company names is for the benefit of the reader; such use does not constitute an official endorsement or approval of any service or product by the U.S. Department of Agriculture to the exclusion of others that may be suitable.

Guidelines for Measuring the Physical, Chemical, and Biological Condition of Wilderness Ecosystems

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and
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Betsy Hood,
Science and Policy Associates, Inc.**

¹Research reported here was funded by the Rocky Mountain Forest and Range Experiment Station under a contract with Science and Policy Associates, Inc. The Station's headquarters is in Fort Collins, in cooperation with Colorado State University. Supervision was provided by Douglas G. Fox, Chief Meteorologist and Project Leader for The Research Work Unit, Effects of Atmospheric Deposition on Natural Ecosystems in the Western United States.

Foreword

This report is the product of an effort to poll the scientific community about the most appropriate techniques to be used to measure the condition of wilderness ecosystems. These techniques recognize the constraints imposed by the statutory designation of wilderness. They are focused on monitoring needed to support the air resource management responsibilities of the Forest Service and other managers of Class I areas, as mandated by the Clean Air Act.

This report was prepared as part of a contract effort between the Rocky Mountain Forest and Range Experiment Station, and Science and Policy Associates, Inc. of Washington, D.C. SPA crafted a process that included a large group of scientific talent (listed at the end of the Guidelines) organized to develop a consensus product with an ever-widening group of interested parties. These Guidelines specifically result from a formal public review of earlier drafts. Review comments and the responses to them are available from the Rocky Mountain Station.

Readers should keep in mind that wilderness monitoring is complex and controversial. Improvements are likely to result only through experience with the application of these guidelines in diverse locations over the breadth of ecosystems that populate the Wilderness system in the US. Toward that end the Rocky Mountain Station is continuing to develop and record experiences with the application of these Guidelines. Three specific examples are worth mentioning:

1. The Wyoming State Office of the USDI Bureau of Land Management is applying the Guidelines to selected wilderness study areas in the western part of the State and evaluating their utility. This work was initiated in 1987 and will be ongoing for 5 years.

2. The Idaho National Engineering Laboratory, a national laboratory under the Department of Energy, is conducting a 2 year technical review and critique of the Guideline methods. INEL work is focused on the Bridger Wilderness.

3. The Atmospheric Deposition Effects research unit at the Rocky Mountain Station is conducting continued long term study of wilderness ecosystems using both direct stress/response and general biogeochemical procedures. A focus of this research is to

provide Federal land managers and regulators with tools to discharge appropriate and effective management of air resources as one of the multiple natural resources of wilderness.

Thus, we recognize that the guidance provided in this report will need periodic review. It is likely that versions of these Guidelines will be updated every 5 years.

The Need for Guidelines

Guidelines for determining current conditions of sensitive resources in Wilderness ecosystems have several purposes. FLMs and regulators need implementable measures to determine if significant changes are occurring in Wilderness areas in order to comply with the law and effectively steward these resources. Air quality decisions must be made now; they cannot await full scientific understanding or development of ideal measurement and monitoring techniques. Information concerning current conditions also will be valuable in fulfilling FLMs' broader stewardship functions for these special areas.

Guidelines are essential to the FLMs' air quality and management missions as well as to the process of sound scientific research. Standardized methods are crucial so that comparable data are produced from different studies and sites. Guidelines help ensure reproducible results and document the procedures used so that future efforts can be related to old data. Uniformity of technique also is critical for appropriately extrapolating results. Scientifically credible protocols provide the needed basis for making sound regulatory, legal, and management decisions.

One final note: These protocols were originally developed to apply to alpine and subalpine ecosystems in areas where the air quality is considered to be clean. Following their development it became clear that many of the measures recommended were more generally applicable. Nevertheless, caveats restricting the protocols to alpine and subalpine conditions are widespread in the document. The reader is cautioned to use the protocols accordingly.

Douglas G. Fox

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Guidelines for Measuring the Physical, Chemical, and Biological Condition of Wilderness Ecosystems

Douglas G. Fox, J. Christopher Bernabo, and Betsy Hood

INTRODUCTION

Background

This report presents appropriate scientific protocols to measure current conditions of air quality related values (AQRVs) in Wilderness areas. These protocols are intended to be guidelines for quantifying the existing status of AQRVs, monitoring for changes from these existing conditions, and subsequently, evaluating whether the changes are naturally occurring or the result of man-caused air pollution/chemical deposition. Certain regulatory and management requirements have constrained the development of the protocols presented in this report. These constraints are explained fully in the first section.

The scientists and contributors that developed this document (listed at the end of these Guidelines) were divided into six work groups, with the Work Group Leaders responsible for the development of protocols for the five technical areas: 1) Atmospheric Environment, 2) Soils and Geology, 3) Aquatic Chemistry and Biology, 4) Vegetation, and 5) Regulatory and Management Constraints. A sixth group, Government Applications, was added shortly after the project began.

A meeting was held in Fort Collins, CO in January 1986 to bring scientists developing the protocols together with some of the federal land managers (FLMs) and regulators who will be the users of the guidelines. Discussions of draft lists of measures resulted in substantial progress toward consensus. After further internal review of the lists, the Work Groups began to prepare their draft protocols.

A second meeting was held in June 1986 to 1) provide an opportunity for the project team to refine the draft protocols; 2) widen the sphere of participation in reviewing and refining protocols by involving additional key external users and scientists; and 3) aid in a smooth transition to the larger consensus development meeting, the Public Review. Consensus building among diverse stakeholders and other interested parties is an important component of this project. Involving key industry, state, federal, and environmental groups prior to the public review meeting enabled the Work Group Leaders to address emerging technical concerns early in the process.

The final task of this phase of the project was the Public Review of the draft document. As part of this process, a Public Review Meeting, announced in the Federal Register, was held in Boulder, CO in December 1986. The purpose of this meeting was twofold: 1) to educate the participants on FLMs' needs and regulatory and management constraints, and 2) to allow review

and discussion on key technical issues, and to develop consensus on these issues. The comments received during this meeting, and written comments from the comment period following the meeting, were addressed by the Work Group Leaders during the final revision of this document.

Protocol Development

Several basic project assumptions were discussed and clarified at the June meeting to provide guidance in the preparation of these protocols:

1. The protocols are being developed initially for application to high-elevation western areas.

2. The measurements and protocols will be used by FLMs and air quality permitting authorities specifically for the protection of "air quality related values" of national Wilderness areas designated as class I areas under the Clean Air Act.

3. The measurements are not intended to be research project, but will be conducted to fill specific resource management regulatory information needs.

4. In most cases, the land manager's/permitting authority's needs will be met by the measurement of change in the most sensitive component of the ecosystem. The determination of whether a change is adverse is the responsibility of the FLM.

Not all possible attributes can be measured, and the list must be parsimonious and practical. An attribute should have ecological significance and should be likely to change as a consequence of air quality effects. Ideally, it should change only in response to changes in air quality, and nothing else; clearly an impossibility! The attribute measured and the method of measurement must be defensible to a consensus of the scientific community. Non-destructive methods are preferable, not only because of Wilderness regulations but also because repeated measurements of the same organism or assemblage is advantageous. Attribute variables that can be monitored with low frequency should be given consideration over those that require many measurements at intervals of less than one year. Only those attributes that can be readily measured with high accuracy should be considered.

Problem

There are several important reasons for systematically establishing guidelines for methods and techniques for monitoring current AQRV conditions and tracking future condition changes. These reasons include the following:

1. To provide clarity internally for the

Forest Service in Wilderness management, planning, operations, and decisions, and externally to States and prospective new air pollution sources about what the FLM considers necessary in monitoring the current conditions of certain AQRVs and potential air pollution-caused changes in those AQRVs;

2. To reduce the period of time needed to complete AQRV impact analyses during the air quality permit review process;

3. To provide a standardized approach to AQRV impact analysis so that analyses by different parties can be compared, and so that analyses in different permitting cases can be compared with one another;

4. To provide a framework for due process with respect to both the Forest Service's AQRV impact analyses and findings and its broader Wilderness protection mandate, thus enhancing the defensibility of such analyses and findings in regulatory and judicial proceedings; and

5. To the extent feasible, to minimize conflicts over technical issues surrounding AQRV sampling, monitoring, and measurement, thus limiting disagreement where possible to value judgments about whether a projected AQRV effect is considered an "adverse impact."

General Issues

Guidelines of several types are needed. First, however, it must be established what should be measured to gauge man's impacts on ecosystems. Techniques and sampling and analytic procedures then must be determined that are appropriate to the physical, regulatory, and management constraints of Wilderness areas. These constraints include rugged, remote, often high-altitude settings subject to extreme physical conditions; Wilderness Act statutory and related regulatory prohibitions; Clean Air Act requirements for permitting; and management constraints such as budget limitations.

Major problems only touched on in these guidelines, but still requiring further consideration, are:

1. Sampling intensity and location are key variables that must be determined, given the degree of natural variability and physical limits on practical measurements. Not only in-depth knowledge of the natural systems, but also statistical design considerations bear on this issue. Technical approaches must be developed for the most practical and representative ways to make the required measurements in Wilderness areas. Guidelines are needed for both on-site and laboratory analysis so that sources of error can be minimized. A major challenge is designing sampling schemes that can adequately represent the diverse physical, chemical, and biological variables.

1. Guidelines also are needed for data reduction, analysis, and archiving. These post-measurement treatments of data and samples are an important consideration for developing results that will still be useful in the distant future. A quality assurance plan should be developed along with the other protocols to ensure reliable and meaningful results. Quality assurance/quality control (QA/QC) is essential to

characterize adequately the sources of error and the inherent uncertainties in the data collected.

2. Major concerns are how to address the inevitable tradeoffs between what measurements ideally are desirable scientifically and what is actually possible under the physical and legal constraints imposed by high-elevation Wilderness sites and limited resources. It could be argued that not enough is known even to determine what to measure, when, or how. This approach is not a luxury that FLMs can indulge. The task at hand is the art of the possible; the immediate goal is to determine the best possible approach, fully document it, and then proceed to use it knowing it is not ideal.

The guideline protocols presented within this document are not intended to represent all that can be measured within Wilderness ecosystems. Conversely, not all of the measurements suggested here may be necessary for a given site or situation. These protocols are presented as a reasonable list of measurements for establishing current conditions in alpine and subalpine areas to aid in detecting changes in the future. In addition, a mechanism must be provided for the integration of data collected on aquatic chemistry and biota, catchment soils, vegetation, and atmosphere. This integration will be critical to maximize confirming evidence for measured effects.

The high degree of scientific uncertainty about how atmospheric chemicals influence natural ecosystems means no single widely accepted view exists on many issues. Consensus building must be part of the entire process so that the greatest degree of scientific credibility possible can be achieved. Part of the purpose of this project is to educate the research and technical community on what the FLM needs are, the reasons the FLM cannot wait for ideal approaches to be developed, and the legal and management constraints under which the FLM must act. The best current scientific judgment must be made, discussed, and agreed on to accomplish our goals.

Organization of Document

The first section of this document presents the paper prepared by Work Group 5, Regulatory and Management Constraints. The following sections present each set of protocols developed by Work Groups 1 through 4. The members of the Work Groups, including those in Work Group 6, Regulatory Applications, are listed on page 48, at the end of these Guidelines.

REGULATORY AND MANAGEMENT CONSTRAINTS

This chapter briefly explains constraints on development and application of scientific guidelines for the measurement and analysis of "air quality related values" (AQRVs) in wilderness areas. These constraints are imposed by the Clean Air Act (CAA) and the Wilderness Act (WA), the physical location of remote areas, weather, altitude, and other such factors. The measures included in this document have been

shaped and limited in their approach by the constraints identified here. Therefore, this chapter is intended to assist readers in developing a full understanding and appreciation of the possible constraints on the development and implementation of the guidelines.

Clean Air Act Context

The Clean Air Act Amendments of 1977 included a program for prevention of significant deterioration of air quality, generally referred to as the "PSD" program. In part, this PSD program was intended to safeguard the air quality related values (AQRVs) of Wilderness areas and National Parks which the statute designates as "Class I areas." This "Class I" designation allows only very small "increments" of new pollution above already existing air pollution levels within the area, and subjects each such area's AQRVs to special protection considerations under the Clean Air Act.

Under the CAA, the appropriate Federal Land Manager (FLM) is charged with an "affirmative responsibility" to protect the AQRVs of Class I areas from adverse air pollution impacts. In the case of the Forest Service, the FLM's affirmative responsibility to protect AQRVs has been delegated to the Regional Forester level.

The FLM's "affirmative responsibility" is implemented, in part, through the PSD new source review process, a preconstruction review and permitting program for major new or expanding sources of pollution. Any major facility seeking a new source permit for location or expansion in a Clean Air area must meet several requirements, among them the Class I and/or II increments, the so-called AQRV "adverse impact test," and the Best Available Control Technology (BACT) evaluation. In the PSD permitting process, the FLM determines whether a proposed source's emissions will have an adverse impact on Class I AQRVs.

New source permit applicants submit plans to the permitting authority, who examines the proposed location of the facility, its general design, projected air pollution emissions, and potential impacts. When a proposed source's emissions may have an impact on a Class I area, the permitting authority (EPA, or the State, if EPA has delegated PSD authority to that State) alerts the Federal Land Manager. The FLM then conducts an "adverse impact determination" to assess the impact the projected pollution level increases would have on the Class I area. The application review process may take as little as 30 days or, with complex or controversial projects, possibly longer than 1 year. The FLM's adverse impact determination must be completed within this period.

Wilderness Act Context

Legal Direction for Managing Wilderness

Congress established the National Wilderness Preservation System in 1964 "to secure for the American people an enduring resource of wilderness." The Wilderness Act describes the basic purpose of wilderness, defines the

wilderness resource and character, and establishes management direction to preserve an enduring wilderness resource. This direction is the foundation for the implementing regulations, found in 36 CFR 293, 36 CFR 291, and Forest Service policy in FSM 2320.

The preservation of wilderness character means striving to preserve "untrammelled" natural conditions and "outstanding opportunities for solitude." This meaning applies to all wilderness management activities, including resource monitoring of all kinds. Minimizing the effects of human use or influences on natural ecological processes is the most important principle of wilderness management. To clarify management direction, the Act spells out specific prohibitions, while allowing only minimum necessary exceptions:

Except as specifically provided for in this Act, and subject to existing private rights, there shall be no commercial enterprise and no permanent road within any wilderness area designated by this Act and, except as necessary to meet minimum requirements for the administration of the area for the purpose of this Act (including measures required in emergencies involving the health and safety of persons within the area), there shall be no temporary road, no use of motor vehicles, motorized equipment or motorboats, no landing of aircraft, no other form of mechanical transport, and no structure or installation within any such area. [Section 4(c)]

Forest Service wilderness managers must be the leaders in demonstrating that wilderness management tasks (including monitoring of air pollution impacts on resources) can be done without structures, installations, or the use of motorized equipment. The exception is to be granted only when it is clearly shown there is no other feasible way to gather information.

Criteria for Considering Exemptions to Prohibitions

Measurement protocols that require exemptions to the prohibitions against structures, installations, and motorized equipment in wilderness areas are not likely to be considered favorably. The criteria for considering exemptions are found in the Forest Service Manual in the following sections:

Structures - 2324.3. This section sets criteria that are intended to limit structures to "those actually needed for management, protection, and use of the wilderness for the purposes for which the wilderness was established." This section also requires documentation of need for structures, schedules for their removal, and sets specific standards for materials and siting.

Research - 2324.4. While "encouraging research in wilderness that preserves the wilderness character of the area," this section requires that research proposals be reviewed "to ensure that research areas outside the wilderness could not provide similar research opportunities" and "to

ensure that research methods are compatible with wilderness values." Further, it requires specific use stipulations in the approval document. Requests for exemptions to wilderness access/user restrictions cannot be based on economic costs to, or the convenience of, the researchers.

Motorized Equipment and Mechanical Transport - 2326. In an effort to "exclude the sight, sound, and other tangible evidence of motorized equipment or mechanical transport within wilderness," this section lists the specific criteria for exemption from prohibitions on the use of motorized equipment and mechanical transport in wilderness.

In all likelihood, then, a request for an exemption is likely to be refused unless it can be demonstrated unequivocally that the data to be gathered under the exemption are absolutely necessary, and all possible alternatives to the exemption have been considered.

In conclusion, the Wilderness Act and the Forest Service regulations require the use of scientific protocols and measurements that protect wilderness values. This means that the measurements either must be easily obtainable within the wilderness by primitive means, or be obtained from representative sites outside the wilderness.

Some Specific Constraints Considered in Protocol Development

The following are examples of specific factors and issues that have constrained and shaped the development of protocols.

1. No guidance is given in the CAA as to how much advance notice the FLM must be given by the permitting authority to allow proper assessment of potential AQRV impacts of a proposed new source of air pollution. Although the FLM may have more than a year, in practice he may have as little as 30 days for conducting this analysis. Thus, FLM may not be free to begin a monitoring study after he is presented with the permit application. To be useful in the permitting process, data must have already been collected under the protocols. Moreover, the data must

have been gathered over a sufficient time period to establish meaningful current conditions of the resource in question.

2. The types of AQRV measurement and analysis that can be performed may be seriously constrained by certain physical and environmental factors in the alpine and subalpine setting. These factors may include weather, season, animal damage, remoteness, and lack of power.

3. The AQRV analyses likely will be constrained by a lack of skilled personnel and funding. In general the protocols call for monitoring efforts that are simple and cheap, use current state-of-the-art methods and equipment, and do not push the boundaries of technology.

4. Because the results of AQRV analyses are to be used in the new source permitting process (and, potentially, in subsequent judicial review) a premium is placed on the reliability of the results and the subsequent ability to make and defend "yes" or "no" decisions concerning whether a proposed source will cause an adverse impact.

5. The ranges of uncertainty in determining potentially measurable changes in AQRVs (or in determining the significance of any given change) as the result of proposed source emissions should be clearly identified and described. The implications of such uncertainty should be described adequately for nontechnical decision makers.

Conclusion

The constraints of the Clean Air Act, the Wilderness Act, management considerations, and the physical and environmental factors seriously limit the types of AQRV measurement and analysis that may be performed in wilderness areas. Guidelines were developed within these constraints to insure realistic and feasible techniques. Some compromises have been necessary between "ideal" or "preferred" AQRV measurement and analysis techniques and those which are deemed "adequate" for management and regulatory purposes. Therefore, the guidelines may be less than "state-of-the-art." Nonetheless, these guidelines and techniques are intended to be scientifically sound and accurate enough for reliable determinations of the current condition of the area's air quality related values.

Atmospheric Environment

Purpose

A major objective of this atmospheric component of these guidelines is to establish a reference for assessing the impact of airborne pollutants on sensitive ecosystems. To meet this objective, this guideline includes measurement methodology for the ambient concentration of certain gases and aerosols, and for the concentration of pollution-related ions in precipitation and snow pack. Dry and wet deposition of pollution-related material can be inferred from these ambient measurements.

Dry deposition fluxes can be computed by multiplying the ambient concentration of the pollutant above a surface by its deposition velocity, which is assumed to vary with land surface type, time of day, season, and several other factors. Meteorological measurements will therefore accompany the ambient concentration measurements. This approach represents a highly empirical parameterization that relies heavily on a relatively sparse data base of dry deposition measurements.

Wet deposition can be estimated by multiplying the precipitation-weighted ion concentration by the total amount of precipitation, the latter measured by standard meteorological means. During the cold season, snow pack measurements may be necessary for both wet and dry deposition estimates.

Because of the difficulties of making aerometric measurements within a Wilderness, one or more sites will be established at the boundary of the Wilderness, where the inflow and outflow of pollution-related material can be monitored. Within the Wilderness area, passive monitoring techniques can be used such as measuring the total amount of precipitation, measuring the total snow pack depth, retrieving representative snow pack samples for laboratory analysis, and establishing a detailed inventory of land surface type.

The proposed protocols will provide estimates of airborne pollution material. Compliance with pollutant regulations or with allowable air quality increments under prevention of significant deterioration (PSD) regulations is not being examined. These guidelines will not of themselves establish air quality baselines for permitting new sources under the Clean Air Act.

The guidelines make maximum use of existing procedures and methodologies that have been, or are being, field tested as part of a national network.

Several critical assumptions have been made during the development of the atmospheric component of the guidelines. These include:

1. Procedures and measurement methodologies to evaluate compliance with existing standards for criteria pollutants are not discussed. The concentrations for gases and particles within a Wilderness area are expected to be well within existing standards. A notable exception may be

ozone; its continuous measurement is therefore recommended at all sites as required for compliance testing. Should the need evolve for compliance testing based on preliminary assessments, taking into account results from model calculations and other efforts, then the methodologies published in the Federal Register by the EPA will serve as protocols.

2. Models can be used for guidance in selecting regionally representative sites.

3. The meteorological and aerometric measurements should be expanded spatially and temporally if the representativeness of these measurements is in doubt. Aircraft sampling over the Wilderness area and vertical profiles for meteorological data are powerful tools for documenting regional air quality.

4. Although large particle deposition results in significant chemical input to ecosystems, we assume that such particles are primarily from local natural sources and hence not man-caused. Thus no measures are suggested at this time.

Warm Season Measurements

Gases and Aerosols

Table 1 summarizes the aerometric parameters that are measured in this protocol. Our knowledge of trace gas and aerosol exchange between the atmosphere and the earth's surface is limited to a small number of gases (mainly ozone, NO₂, HNO₃, SO₂, and NH₃). This guideline suggests dry deposition may be

Table 1.—Aerometric measurements.

Analyte	Measurement method	Time resolution	Quantitative detection limit (QDL)	Desired accuracy
O ₃	uv photometry, automatic	hourly	5 ppb	1gr of QDL or 10%
NO ₂ ¹	filter pack (TEA-impregnated filter following Teflon and nylon)	day/night ² (12 hr each) for up to 1 wk average	0.1 ppb	1gr of QDL or 20%
Mass, SO ₄	filter pack (Teflon)	day/night ² (12 hr each) for up to 1 wk average	0.2 ppb	1gr of QDL or 20%
Inorganic nitrate	filter pack (Teflon, nylon)	day/night ² (12 hr each) for up to 1 wk average	0.2 ppb	1gr of QDL or 20%
Total ammonia	filter pack (oxalic acid-impregnated filter following Teflon)	day/night ² (12 hr each) for up to 1 wk average	0.2 ppb	1gr of QDL or 20%
SO ₂	filter pack (K ₂ CO ₃ -impregnated filter following Teflon)	day/night ² (12 hr each) for up to 1 wk average	0.2 ppb	1gr of QDL or 20%

¹Optional.

²With the option to measure over a 24-hr period only.

calculated from measured ambient air concentrations. Actual deposition is inferred from concentration data and deposition velocities that have been determined for specific gases and surfaces. The following trace materials are measurement candidates:

Sulfur dioxide (SO_2) is a key primary pollutant of concern in Wilderness. Dry deposition of SO_2 , especially to moist surfaces, is considered a major sink, perhaps the major sink of this species. Uptake of SO_2 by vegetation and ecosystems is an acid-producing process.

Nitrogen dioxide (NO_2) is phytotoxic and hence of direct concern in Wilderness. This gas is relatively insoluble in water, but is highly reactive with biological materials. Chamber studies as well as field measurements indicate that NO_2 can dry deposit at moderate rates.

Ozone (O_3) is formed in the atmosphere as a product of reactions involving hydrocarbons and nitrogen oxides. This connection with nitrogen oxides alone establishes its importance to Wilderness. Ozone has been demonstrated to be phytotoxic. Dry deposition is a major sink of O_3 ; ozone is probably the best studied air pollutant for this reason. All of these reasons place O_3 as high priority for measurement.

Nitric acid (HNO_3) is the final product of atmospheric oxidation of nitrogen oxides. It is a strong acid, highly soluble in water. Nitric acid is thought to be dry-deposited at a high rate, governed by atmospheric turbulence. The high acidity of HNO_3 , as well as its role (often the case with nitrogen compounds) as a plant nutrient, establish the importance of characterizing its dry deposition.

Ammonia (NH_3) is not considered a direct pollutant. Sources of NH_3 are principally biological: animal wastes, fertilizer, etc. NH_3 is of interest in the Wilderness area context because it is one of the principal atmospheric bases available to neutralize atmospheric acids. However it can contribute to soil acidification when taken up by vegetation. Reactions of NH_3 with aerosol H_2SO_4 result in gas-to-particle conversion that in turn affects the deposition and fate of NH_3 . Additionally, NH_3 , as an available nitrogen species, is a nutrient to nitrogen-poor ecosystems. Little is known about dry deposition velocities of NH_3 , but they may be large in view of the high solubility of NH_3 at acidic to neutral pH.

Aerosol particles are a prime cause of visibility reduction as well as the means by which acidic material is delivered and hence are of considerable concern in Wilderness. Most of the sulfate and nitrate associated with atmospheric particles is found on particles of 0.05 to 5 micron diameter, as a result of gas-to-particle conversion. Because these particles can travel over long distances (because of their low gravitational settling velocities), they are good indicators of distant pollution sources, particularly of sulfur dioxide.

Wet Deposition (Quality and Quantity)

Table 2 lists the parameters to be measured

in precipitation. Wet deposition is a major pathway for the transport of nitrogen and sulfur compounds to the earth's surface. Wet deposition combined with dry (gases and aerosols) represents total deposition. Thus precipitation quality and quantity is of major importance in determining pollution impacts on ecosystems. Because of the remote location of Wilderness areas from major pollution sources, a significant fraction of the total deposition of pollution-related material will be delivered as "wet" deposition.

Several national wet deposition networks have been in operation for several years. The installation, operation, and subsequent laboratory analyses are well established and are adapted for this protocol. All of the analyses listed in table 2 can be conducted at a central laboratory. The only variables measured at the monitoring site after precipitation collection (or within a few hours driving distance from the monitoring site) are precipitation quantity, field pH, and conductivity.

Meteorological Measurements

To assess total deposition, both wet and dry, a series of meteorological measurements are required. Meteorological variables to be measured at a representative site (outside the Wilderness area) during the warm season include

Table 2.—Summary of analytes, analysis methods, and detection limits for precipitation

Analyte	Method	Time resolution		Quant. detection ¹ limit (mg/l)	Desired accuracy ²
		Warm season	Cold season		
H^+	electrode	weekly ave	accumulation over season	—	0.05 pH units
Total alkalinity	titration	weekly ave	accumulation over season	—	20%
Conductivity	bridge	weekly ave	accumulation over season	—	20%
SO_4^{2-}	IC ³	weekly ave	accumulation over season	0.2	1gr of QDL or 10%
NO_3^-	IC	weekly ave	accumulation over season	0.2	1gr of QDL or 10%
Cl^-	IC	weekly ave	accumulation over season	2.0	1gr of QDL or 10%
NH_4^+	AWC ⁴	weekly ave	accumulation over season	0.5	1gr of QDL or 10%
Na^+	AA ⁵	weekly ave	accumulation over season	0.2	1gr of QDL or 10%
K^+	AA	weekly ave	accumulation over season	0.2	1gr of QDL or 10%
Ca^{2+}	ICP ⁶	weekly ave	accumulation over season	0.2	1gr of QDL or 10%
Mg^{2+}	ICP	weekly ave	accumulation over season	0.2	1gr of QDL or 10%

¹Defined as the minimum value that is likely to be detected by the stated method when applied to actual precipitation samples. This value is larger than the minimum detection limit that is achievable in the laboratory for pure standard solutions.

²Defined as the maximum difference between the measured and true value of the quantity in question.

³Ion chromatography.

⁴Automated wet chemistry.

⁵Graphite furnace/Atomic absorption.

⁶Inductively coupled plasma spectroscopy.

temperature, pressure, precipitation, wind speed, wind direction, surface wetness, and relative humidity. Precipitation quantity is a particularly important meteorological variable; wet acidic deposition calculations are very sensitive to estimated precipitation amounts.

Precipitation data measured at a single Wilderness area station during the warm season cannot be representative of precipitation over the entire area. It is important to consider other mechanisms to collect precipitation data within the Wilderness. Because topography and ground cover vary widely in these areas it is not possible to estimate how many collection points might be required in general. It may be possible to estimate the amount of precipitation over the Wilderness area from these combined data, but the reliability of any such effort will depend upon the intensity and frequency of the sampling. Questions such as sampling design and reliability and representativeness of the data are not addressed in this document.

Wind data are collected at the same location to provide information necessary for understanding the variability in the aerometric and precipitation chemistry data, as this variability often can be attributed directly to sources upwind. Pressure and temperature data are needed for calculating volume flow rates for aerometric samples. Temperature and humidity data may be needed, along with land use data, vegetation cover data, surface wetness, and other parameters, to estimate dry deposition rates. Meteorological data are also useful for modelling studies that may be required in support of data assessment.

The instruments proposed for this Wilderness area program are listed in table 3. The accuracies specified by the manufacturers are noted. This equipment has been field tested and has been routinely used in many monitoring programs. No recommendations are made for a specific manufacturer; other instruments may have equally satisfactory performance characteristics.

Cold Season Measurements

Table 2 lists the analyses to be conducted on snow pack samples. The snow pack provides an accumulation and integration of deposition events of natural and anthropogenic water-soluble and particulate inputs. Total deposition of pollution-related material averaged over the entire cold season (wet and dry) can be estimated for selected sites within the wilderness area, provided that snow melt occurs only during the normal spring melt period and not intermittently during the winter. Because of the inaccessibility of most parts of the wilderness area during the cold season, seasonal total deposition may be the only measurement parameter obtained during this season.

Depending on the accessibility of the warm season monitoring site, measurements of gases and aerosols should continue during winter. The measurement of "wet" precipitation by use of the wet-only sampler depends on the ability of the sampler to operate effectively under existing

Table 3.--Recommended meteorological equipment list, warm season.

Parameter	Measurement Method	Range	Accuracy
Wind speed	Cup anemometer	1-40 m/s	0.2 m/s up to 13 m/s, and not exceeding 0.5 m/s thereafter
Wind direction	Vane	0-540 degrees	1-2 degrees
Temperature	Two element composite linear thermistor	-30 to +50° C	1° C
Relative humidity	Dielectric polymer capacitance	0-100%	2%
Pressure	Capacitance aneroid	600-1100 mb	0.3 mb
Precipitation ¹	Weighing mechanism	0-15 cm	0.01 cm
Surface wetness	Leaf wetness grid	resistance measurement	

¹At sites where a significant fraction of the precipitation is in the form of snow, an Alter-type windshield will be added.

weather conditions. Meteorological measurements should continue throughout the cold season.

Requirements

Sampling Program for Warm Season

In principle, the monitoring sites cannot be located within the wilderness area. The number of required sites depends on the wilderness area under investigation. The equipment measurements detailed here are on a per station basis. A further assumption is that a qualified central laboratory(ies) will be responsible for preparing all required materials (filters, collection bottles, shipment containers, etc.) for the field sites and analyzing the exposed filters and collected precipitation samples. The equipment needs for such a central laboratory are not detailed here, but table 4 presents an overview of the expected concentrations in samples as a function of various analytical techniques available for the analysis of both impregnated filters (from filter pack) and precipitation samples (rain and snow). Table 5 summarizes the instrumentation requirements for the monitoring site. All equipment or support items except the filter pack are readily available from several manufacturers. All equipment and field procedures for precipitation and snow pack samples should be (to the maximum extent possible) identical to existing national or State programs to insure maximum data compatibility.

No standardized equipment for filter pack systems is in use today. Both EPA and EPRI are planning the deployment of filter pack systems in 1987 as part of a nationwide gas sampling network to measure ambient concentrations. The equipment discussion that follows assumes such networks will be implemented, and filter pack equipment (with impregnated filters) or annular denuders will become commercially available for this wilderness area monitoring protocol.

The filter pack air sampling method uses

Table 4.—Expected concentrations of rainwater contaminants, laboratory detection limits for selected constituents in rainwater and filter packs (min. detection level, MDL, in ug/ml, precision in %).

Observable	Typical Concentration Range (ug/ml)		IC ^C	AC ⁴	ICP ⁵	AA ³	XRF ⁶	Electrode ⁷	Titration ⁸
	Rural	Remote							
SO ₄ ²⁻	3.4 ¹	0.8-1.2	0.025/5%	0.3/5%			0.04/2% (S)		
NO ₃ ⁻	2.3 ¹	0.7-1.0	0.015/5%	0.04/5%				0.4/5%	
Cl ⁻	0.64 ¹	0.15 ²	0.007/5%	0.02/5%			0.02/2%	1.8/10%	
NH ₄ ⁺	0.39 ¹	—	0.011/5%	0.005/5%				0.015/5%	
Na ⁺	0.31 ¹	0.085 ²	0.007/5%		0.002/10%	0.002/2%	0.05/2%	6.02/5%	
K ⁺	0.088 ¹	0.02-0.04	0.016/5%			0.01/2%	0.01/2%	0.04/5%	
Ca ²⁺	0.21 ¹	0.2-0.5			0.00007/5%	0.01/2%	0.007/2%	0.02/5%	
Mg ²⁺	0.057 ¹	0.03-0.08			0.00005/5%	0.001/2%	0.04/2%		
H ⁺	0.074 ¹	—						± 0.1 unit	
Total acidity	0.11	—							0.002/3%
Conductivity	0.7 umhos	—							0.1 umhos/<10%

¹Average of 8 sites. MAP3S/RAINE 1982.

²NADP/NTN sites.

³Desert Research Institute Lab results.

⁴Technicon, Inc. specified limits.

⁵Fassel and Knisely 1974.

⁶Assumed 47 mm filter, 5 ml rinse using protocol 5 detection limits as specified by NEA labs.

⁷Orion specific ion electrode, MDL as specified.

⁸Monthly average values from Chan et al. 1983.

selective filters within the filter pack to collect specific pollutants over a 12-hour to 7-day period, depending on protocol. The filter packs are sheltered in a sample head, which is permanently attached on a support pole at a height of 7 meters.

With this pack of sequential absorbing filters, the average concentration (12 hr up to one week) of fine particles (SO₄, NO₃, NH₄) and gases such as SO₂, HNO₃, NO₂, and NH₃ can be monitored. When the airstream is drawn through a size selective inlet, particles of a specified size range can be captured. Various choices exist for the selection of filter media, absorbent, flow meters, and size selective inlets. Although filters are not considered an equipment item, they are discussed because they are an essential part of the system.

Particles. Teflon membrane filters will be used to collect the particles before the air stream encounters other filters. A cyclone is included prior to all filters to remove particles larger than approximately 2 µm, and a short length of Teflon tubing is used as a transition flow reactor for the flow before encountering the filter (Knapp, et al. 1986, Durham, et al 1986). Teflon has been shown to quantitatively pass HNO₃ (Goldan et al. 1983), although nitrate particles collected on the filter may volatilize (Appel et al. 1984). Although these filters are analyzed only for sulfate and nitrate as part of the wilderness protocol, they are selected and sectioned so that more extensive chemical analyses can be performed on them at some later date. (X-ray fluorescence analysis for elemental species might be useful, for example.) This may be useful for visibility considerations.

Nitric Acid and Ammonia. Nylon membrane

filters are used to capture nitric acid (HNO₃). The specificity of nylon for HNO₃ capture has been demonstrated in both laboratory (Miller and Spicer 1975, Spicer et al. 1978) and field studies (Spicer et al. 1982). Nylon does not remove NO₂ or PAN but may absorb N₂O₅ at high humidities. When located downstream of the Teflon filter, it also absorbs any HNO₃ and some of the SO₂ that may be volatilized from the particulate collection. Nylon membrane filters (Nylasorb) have been used to trap nitric acid quantitatively (Spicer 1979). Recently, citric acid coated glass-fiber filters have been recommended for collection of ammonia (NH₃) as a backup in the filter pack system. This allows the collection of any ammonia formed from ammonium nitrate particles collected upstream (EPA 1987).

Nitrogen Dioxide. A glass-fiber filter impregnated with triethanolamine (TEA) absorbs nitrogen dioxide (NO₂). The TEA filter will measure time-averaged low concentration NO₂ (Levaggi et al. 1973, Durham and Ellestad 1984, Knapp, et al. 1986).

Sulfur Dioxide. A K₂CO₃-glycerol impregnated cellulose fiber filter has been shown to be an effective trap for sulfur dioxide (SO₂) (Hugen 1963). A glass-fiber filter impregnated with triethanolamine (TEA) has been used to collect SO₂ (Knapp, et al. 1986).

Various options are available for a system that passes samples of the atmosphere through these filters. For the wilderness area, application of a heated Teflon-coated cyclone that removes particles larger than 2 µm aerodynamic diameter is proposed. Figure 1 illustrates one of these systems (EPA 1987).

The cyclone assembly is housed in an instrument shelter. The cyclone inlet is protected from precipitation but able to sample air directly. A minimum length of Teflon-coated pipe is used to direct the sample streams to the filter packs, located inside the shelter. The mass flowmeters and pump are located in a separate pump box. When replicate sampling is

Table 5.--Summary of basic equipment needs for monitoring site.

Equipment	Time resolution	Man days requirement at site ¹
<u>Warm season</u>		
<u>Precipitation</u>		
Special bucket with lid opened automatically by rain	events averaged over one week	0.4 per week
<u>Aerometric</u>		
Filter pack ² Teflon nylon TEA-impregnated for NO ₂ K ₂ CO ₃ -impregnated for SO ₂ oxalic acid-impregnated	day/night (12-hr schedule) averaged over one week	0.3 per week
Ozone - uv photometry	(1-hr schedule)	0.2 per week
<u>Meteorology</u>		
Wind speed:cup anemometer Wind direction:vane Temperature:resistance thermometer Pressure:capacitance aneroid barometer Precipitation:weighing rain gauge Relative humidity:polymer capacitance sensor	(all 15 min or 1-hr average)	0.1 per week
<u>Support Equipment</u>		
Data logger for meteorology, ozone Triple beam balance pH meter Conductance bridge Calibrator for gas monitor (ozone) Supplies Refrigerator/cooling chest for sample transportation		
<u>Shelter and Tower</u>		
10-meter tower for meteorological instrument and air intake Instrument shelter with AC/heat capable of maintaining temp. Security fence Access road Power access		
<u>Cold season</u>		
<u>Snow Pack</u>		
Standard Federal Sampler	seasonal average collection before snow melt	1 week per station
<u>Support Equipment</u>		
Refrigerator for snow samples Balance Supplies		

¹Exclusive of travel to and from site.²Requires fabrication for samplers, not yet routinely available as an "off the shelf" item.

necessary, a second complete filter pack system and shelter can be co-located.

Filters required for filter pack sampling must meet the following requirements: 1) mechanical stability, 2) chemical stability, 3) low flow resistance, 4) good retention without clogging, 5) low and consistent blank values for the species being measured and those which might additionally be measured, and 6) reasonable cost and availability.

EPA is currently developing protocols for a transition flow reactor (TFR) filter pack as illustrated in figure 1. Interested readers are referred to the authors of this protocol for

further detailed information (Dr. Jack Durham, Atmospheric Sciences Research Laboratory, Office of Research and Development, US Environmental Protection Agency, Research Triangle Park, NC 27711).

Ozone. Ambient ozone (O₃) concentration is measured with a UV photometric type instrument such as a Dasibi Environmental 1003-AH ozone monitor or the equivalent model TECO 49P. The Dasibi UV absorption photometer measures the amount of ultraviolet radiation absorbed by ozone in a sample of ambient air. The quantity of light absorbed is proportional to the concentration of ozone in the air sample. Ozone concentration readings are digitally displayed on the front panel over the range of 0.000 to 1.000 ppm. An analog output of 0-1 VDC also is connected to the data logger.

Gas is continually supplied to the sample chamber by a self-contained pump and handling system. The intensity of the UV beam traversing the sample cell is attenuated in proportion to the ozone concentration in the sample. The signal is electronically processed for presentation by the readout system and output to the data logger. Two reference subsystems provide a high degree of stability by correcting for source intensity, optical path transmittance and detector response changes. Self zeroing and interference removal are accomplished by comparison of sample and reference readings. In the operating parameters of the analyzer are within specifications, no span or zero drift occurs and the analyzer is self-calibrating.

Cold Season -- Snowpack Sampling

Several standardized tools are available for sampling snow cover. Table 6 summarizes the properties of snow samplers used in North America.

Tests suggest that a sharp "Federal sampler" (or equivalent) is suitable for use in most types and depths of snow cover. Cooperative testing by North American agencies through the Western Snow Conference is continuing in an attempt to develop a standard metric sampler that will provide accurate and repeatable measurements for deep and shallow snow covers (Farnes et al. 1980). Currently, the "Standard Federal" is the preferred choice throughout the western U.S. and Canada. Experience indicates that, in deep snow packs (> 4-5 m depth) with numerous ice lenses, the Standard Federal corer is not sufficiently robust for repeated coring during a single field trip. This is especially true for coring in cold, continental snow packs such as those found in the Rocky Mountain region. In such cases, a McCall corer should be used. Cross-calibration to Standard Federal core sampling efficiency has been reviewed by Farnes et al. (1980).

For very dense, deep snowpacks, a combination of a core and a snowpit may be necessary, since it may be impossible to extract the coring tool (Dozier, pers. comm.). Snow pits also allow more detailed examination of the snow. They provide the only practical method of determining layer structure, ice lense structure, and snow microstructure available at the present time. Details of snow pit observations are found in Perla and Martinelli (1976) and Jones (1983).

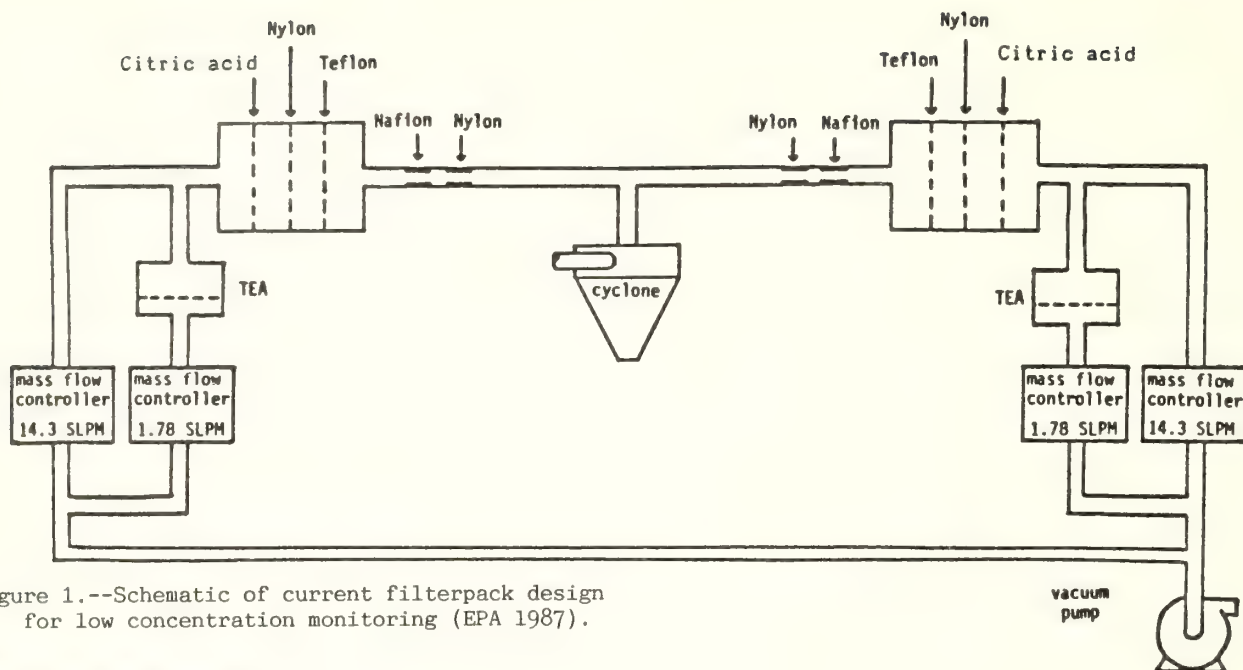


Figure 1.--Schematic of current filterpack design for low concentration monitoring (EPA 1987).

Table 6.--Snow sampler properties.

	Standard ¹ Federal	Federal ²	Bowman ³ L-S	McCall ⁴	Canadian ⁵ MSC	Adirondack ⁶
Material	aluminum	aluminum	plastic or aluminum	heavy gage aluminum	aluminum	glass fiber
Length of tube ⁷ (cm)	76.2	76.2	76.2	76.2	109.2	153.7
Theoretical ID of cutter (cm)	3.772	3.772	3.772	3.772	7.051	6.744
Number of teeth	16	8	16	16	16	None ⁸
Depth of snow that can be sampled (m)	<5	<5	>3.5	>5	1.0	1.5
Retains snow cores easily	yes	yes	yes	yes	no	no

¹Standard sampler used in the Western United States and Canada.

²Identical to "Standard Federal" but has an 8-tooth cutter.

³Cutter has alternate cutter and raker teeth and may be mounted on plastic or standard aluminum tubing. It is more an experimental rather than operational sampler.

⁴Used in dense snow or ice. It is a heavy gauge aluminum tube with 5-cm cutter with straight flukes. It may be driven into the pack with a small slide drop hammer producing an icepick effect.

⁵Atmospheric Environment Service large diameter sampler used in shallow snow cover.

⁶Large diameter fiberglass sampler commonly used in Eastern United States.

⁷Most snow samplers in North America use inches and tenths as their basic units of measurement. Values in this table are corresponding metric equivalents.

⁸Stainless steel circular cutter edge or small teeth.

Note: A special sampler is needed for snow sampling if snow is analyzed for trace metals.

Whether or not the increased information is worth the increased work of digging pits depends on the intended use of the information.

Field Procedures

Sampling Site Selection Criteria -- Warm Season Regional considerations.--Because of the

difficulties in operating monitoring sites within the wilderness area, "representative" locations will be chosen for sites at the periphery of the area. "Representative" in this context refers to the climatology of the region and to the synoptic scale air mass flowing over the wilderness area. Both of these overall meteorological parameters should be assessed in conjunction with man-made pollution sources in a roughly 500-mile zone surrounding the wilderness area to determine approximate locations for potential monitoring site(s). Ideally, such an assessment should yield monitoring site(s) that can characterize the flow of pollution-related material into and out of the wilderness area. The number of monitoring sites must be established on a case-by-case basis, and obviously depends on the size of the wilderness area, the complexity of terrain, the acceptable level of uncertainty, etc. Determining an appropriate number of sites is not an easy task. TAPAS models (Fox, et. al., 1987) are available to aid in this task.

Local considerations.--The most important criterion is the availability of electrical power, because most of the atmospheric samplers require at least 110 V electricity. Within the constraints set by the availability of power, the sampling site should be as close to the remote area of interest as possible. The temporal variation of atmospheric concentrations of interest is probably much greater than the spatial variation, particularly in background locations; however, very little data are available to confirm this speculation.

The selection of the atmospheric sampling site also should depend on potential local sources of pollution. Potential local sources include home chimneys, vehicular traffic, auxiliary diesel generators, and local industrial activities. Seasonal changes in activities producing potential pollution also should be noted.

Because of the size of some of the equipment and the need for servicing on a year-round basis, the site should have reasonable access: one should be able to drive close (0.5 km) to the site during various weather conditions. Ideally, the site should be located where year-round staff are available to service the equipment and change the sampling heads.

The site should be protected from animals and unauthorized human entry. The first line of defense is to locate the site out of normal view. Other ways to protect the site include fencing, signing, or locating at a site with a permanent resident on officially protected property such as a ranger station, a university field station, etc. Experience indicates that the most effective protection of a site is to keep it out of everyday view.

Ideally, the site should have a complete ground cover to minimize resuspended materials and dust from the local area, but should never be under or near overstory vegetation. As a rule of thumb, the diameter of the opening should be about 10 times the average height of the surrounding overstory vegetation. The site should be located so that sampling will reflect, as accurately as possible, the chemical constituency of air masses of fairly large circulation.

Because many sampling sites will not have all of the desirable attributes, some compromises must be made. To evaluate tradeoffs, a systematic decision-making process should be used. For example, site criteria are divided into those which must be met, and those which are desirable. Ranking is based first on "musts", then "wants"; a final decision is made by a group of experts in atmospheric sampling.

Site criteria are summarized in table 7. The instruction manual issued by NADP (NADP 1984a) provides further information regarding the establishment of a wet deposition site using the wet/dry precipitation collector.

Sampling Site Selection Criteria for Snowpack -- Cold Season

Total deposition of pollutant-related material accumulated in snow over the entire cold season will be monitored at sites within the wilderness area. The number of snow cores to be sampled varies with the size of the wilderness area, the extent of ecologically sensitive regions, the complexity of the terrain, and other factors, but a minimum of five samples should be taken at each site. These should be selected to collect maximum deposition.

The snowpack should be sampled at maximum accumulation, but before spring melt starts. These ideal conditions are not always met. The Cascade and Sierra Nevada Mountains have a warm snowpack with temperatures usually near 0°C (Smith 1974). Because of air temperature variations, some melting of the snowpack may occur during the winter, and depending on temperature conditions, rain may fall on the snowpack and percolate through it. Such percolation, if it continues through the entire depth of the snowpack, can leach soluble material from the snow in concentrations disproportionate

Table 7.--Site selection criteria for representative aerometric station (warm season) outside of wilderness area.

General criteria

1. The site(s) should be selected to give samples representative of the wilderness area.
2. The site(s) must be accessible during the warm season in all weather conditions on a daily basis.
3. The site(s) must be located in an area secure from damage by animals or vandals.
4. The site(s) must be serviceable by line power and either have a suitable equipment shelter or have room for a suitable shelter.
5. Sampling site(s) should be situated no closer than 20 km from areas enclosing combined sources larger than 10,000 tonnes/yr SO_x or NO_x.
6. Sampling site(s) should be located at least 5 km from population centers greater than 5,000, at least 10 km from population centers greater than 50,000.
7. All candidate sites must appear to meet the detailed selection criteria listed below.
8. The landowner or custodian must be in full agreement with the intended use of the site (including any restrictions on access or use such as limitation on development) and willing to grant the access and space needed to fulfill the sampling requirement for the lifetime of the network.

Specific criteria

1. All large objects that might contribute to the contamination of precipitation samples must be farther than two times their height from the sample collector or fall below a 30 degree elevation angle when viewed from the collection point.
2. Small objects, such as vegetation or fences, that are of comparable height to the height of the precipitation collector opening must either be farther than two times their height from the collector or be at a distance equal to the height of the collector opening--whichever distance is greater.
3. Whenever possible, the precipitation sample and all intakes to aerometric monitoring equipment must be located a minimum of 250 meters from all public roads or other routing mobile sources of atmospheric pollutants.
4. All sampling sites should be located a minimum of 250 meters from any fertilizer storage areas, feed lots, fuel storage areas, stationary internal combustion engines, or other similar sources of potential contaminants.
5. Sources of dust, such as construction areas and tilled farm lands, should be avoided whenever possible. If this restriction cannot be met, these sources should be kept at least 250 meters from the sample locations.
6. All possible efforts should be made to locate monitoring sites on level, naturally vegetated land or in grassy areas. No site should have a slope greater than 20 degrees from the horizontal.
7. All sites must be accessible by vehicle.
8. All sites must be located outside the wakes of buildings, trees, or abrupt changes in terrain.
9. All sites must have clean, temperature-controlled working area set aside for sample processing. The area should be dedicated to the handling of precipitation samples and it must not contain any potential contaminants.

to those in the snowpack (Johannessen et al. 1980). In addition, atmospheric conditions under which the snow was deposited, the degree and type of metamorphism the snow has undergone, and the intensity of rain and/or melt events all can influence the rate at which impurities can be removed from the snow (Shockey and Taylor 1984). Thus, the snowpack cannot be assumed to accumulate and hold all atmospheric deposition during the life of the snowpack.

To lessen the possibility of rain and melting impacts, sampling sites should be located above the freezing level for the particular geographic region under consideration. Whenever possible,

the sampling sites should be located in the southwestern part of meadows or in open areas where shading minimizes surface melting from solar radiation. At lower elevations, the temperature of the snowpack may reach 0°C and therefore endanger its integrity. Selective leaching of ions from the snowpack can be identified by setting out waterproof boxes of about 2 X 2 m and lined with polypropylene plastic in the fall. Snow cores collected outside the boxes can be compared with cores plus melt water from inside the boxes during the later winter sampling period.

Sample Collection Procedure -- Warm Season

Filter pack.--Every seven days (when samples are removed from the precipitation collector), the filter pack is removed and a new filter pack is installed. The following is a preliminary description of the procedures to be followed. The final protocol will depend on the selection made for the national programs.

1. Check the flow rate as indicated on the sampler control module digital readout. Obtain the actual flow rate from the calibration sheet that corresponds to the indicated value from the sampler. Record this value as the "OFF Flow Rate" in the log book and sample record sheet.

2. Note the time on the data logger display. Record this time as the "OFF time" in the log book and sample record sheet.

3. Lower the sample head by releasing the cam lock at the base of the tower and slowly feeding out the line tied to the tower upright.

4. Remove the filter packs by pulling up on the quick-connect fittings collar. Place the filter packs in zip lock bags.

5. The quick-connect fittings seal themselves off when no filter is installed: this will check the system for leaks. After one minute, check to see that no flow is indicated on the control module digital readout.

6. Install the new filter packs by pushing them into the quick-connect fittings in the base plate. The "sample" filter pack should be installed in the fitting marked SAMPLE and the blank filter pack in the fitting marked BLANK.

7. Raise the tower by pulling on the line attached to the end of the tower upright. Secure the upright into the tower base plate and engage the cam lock.

8. Note the time indicated on the data logger display. Record this time as the "ON time" in the log book and sample record sheet.

9. Check the flow as indicated on the control module digital readout. If necessary, adjust the flow to the value corresponding to a flow rate of 1.5 liters per minute from the sampler calibration sheet. Record this value as the "ON flow rate" in the log book and sample record sheet.

Filter pack handling and shipment.--After removal, the complete filter pack is sealed on both ends with plastic screw caps, placed inside a zip lock bag, tagged, and shipped inside a padded box to a central analytical laboratory. The following information should be recorded in the station log book and on the sample identification tag, which will be attached to the

zip-lock bag containing the filter pack: filter number, side ID number, start date and time, and stop date and time.

Standard Operating Procedures (SOPs) have been developed for all phases of the field sampling collection by EPA and Atmospheric Environment Service, Canada.

Precipitation.--An SOP for the measurement of wet deposition exists for all major national networks. The SOP for NADP/NTN will be adopted here. Operational steps including bucket changing and weighing, sample storage, field laboratory analysis (pH and conductance measurement), shipment and maintenance are detailed in the NADP site operation manual (NADP 1982).

In summary, the NADP/NTN protocol is the following:

1. An aerochem Metric Model 301 wet/dry precipitation collector collects precipitation samples, and a Belfort recording rain gauge measures daily precipitation amounts.

2. Samples are collected weekly.

3. The sample is weighed at the site to determine total precipitation volume. The soil-contaminated portion of sample is carefully removed.

4. A 20 ml aliquot is removed for laboratory and pH measurements.

5. A form is filled out by the site operator describing the sample and the collection characteristics (see fig. 2).

6. The sample is mailed in the sealed collection container along with the sample reporting form to a central laboratory for analysis.

Because of the dilute nature of precipitation samples, handling procedures must be followed carefully to prevent contamination. These procedures are presented in detail in the NADP/NTN manual. This plan is adopted for the operation of the monitoring sites, with the exception of those sections which refer specifically to liaison with the NADP/NTN Central Analytical Laboratory (CAL).

Ozone.--SOPs exist for all aspects of ozone measurement, calibration, and preventive field maintenance. They are detailed in, and part of, the owner's manual supplied by the manufacturer (either TECO or Dasibi). The Mountain Cloud Chemistry Standard Operating Procedures can be used for further guidance.

Snowpack Collection Procedure -- Cold Season

The snow sampler is lowered vertically into the snowpack with a steady thrust downward. A small amount of twisting aids in driving the tube and cutting thin ice layers, but considerable force and twisting of the sampler with a driving wrench may be required to penetrate hard layers of ground ice. Penetration to extract a soil plug helps to prevent the loss of the snow core from the tube, and a trace of soil or litter in the cutter indicates no loss has occurred. A quick comparison of the length of the snow core against measured snow depth will show whether a complete core has been obtained. The amount of compaction of the snow core during sampling will depend on snow conditions. If the snow core

NADP/NTN FIELD OBSERVER REPORT FORM

Send Completed Form With Each Bucket To
The Central Analytical Laboratory

BUik		LD	
DA		NA	
QA		NN	
NS/Exclude		SP	

1. STATION Name _____ ID 		2. OBSERVER Initials Signature _____		3. SAMPLE BUCKET Check One <input type="checkbox"/> Wet-Side <input type="checkbox"/> Dry-Side																																																																																																							
4. BUCKET ON Date MO DAY YR Time 0000-2400 BUCKET OFF Date MO DAY YR Time 0000-2400 These Times Are: <input type="checkbox"/> Standard <input type="checkbox"/> Daylight Savings		5. SITE OPERATIONS <i>Check Yes or No for each item for Wet-Side samples only</i> If No, explain in data Block II, Remarks <table style="width:100%;"> <tr><td>YES</td><td>NO</td></tr> <tr><td><input type="checkbox"/></td><td><input type="checkbox"/></td></tr> <tr><td><input type="checkbox"/></td><td><input type="checkbox"/></td></tr> <tr><td><input type="checkbox"/></td><td><input type="checkbox"/></td></tr> </table> <ol style="list-style-type: none"> Collector appears to have operated properly and sampled all precipitation events during entire sampling period Rain gage appears to have operated properly during the week Collector opened and closed at least once during the week, other than for testing 				YES	NO	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>																																																																																														
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Figure 2.--NADP/NTN field observer report form.

REVISED 2/18/83

becomes blocked or frozen in the tube, preventing snow from entering, the core should be discarded and another sample taken. Snow may freeze in the tube when the snow temperature is below 0°C and the air temperature is above 0°C. When a good snow core has been obtained, the sample is weighed in the tube and the combined weight (in water equivalent units) is read directly with a spring balance. The tare weight of the tube is subtracted to obtain the snow water equivalent.

Figure 3 illustrates a convenient format for recording snow survey information in the field. Such a form also provides documentation of any problems encountered while surveying that may affect the accuracy of the survey and the interpretation of the results.

All snow samples should be double-bagged in polypropylene (after dirt or soil has been carefully removed from bottom), heat sealed, and kept frozen by mechanical refrigeration until they are analyzed in a designated chemical laboratory.

Laboratory Sample Analysis

Filter Pack

Development of an SOP currently is being funded by EPA and EPRI as part of the implementation of a dry deposition network. The SOP will describe the processing of filter samples from initial acceptance testing through laboratory analysis of the filter extracts. The acceptance criteria and the manner in which acceptance testing is conducted will be specified in the SOP. All filters that pass acceptance testing are then weighed, packaged, numbered, and sent to the sampling sites.

Upon receipt at the laboratory, each filter is weighed and a certain fraction (specified by the SOP) is reweighed separately. All filters passing quality acceptance tests are chemically analyzed by laboratory processes analogous to those used for precipitation samples.

The preliminary analytical procedures for extracting and analyzing filter pack samples are

Snow Course No.					
Name _____					
Sampler _____	Date _____				
Station No.	Snow Depth cm	Weight Tube & Core	Wt. Tube Only Before Sampling	Water Equivalent cm	Core Length cm
Total					
Average					
Checked _____	Date _____				

a.m.
p.m.

SNOW SAMPLING: Began _____ Ended _____

Sampling Conditions
(Please check items descriptive of present conditions)

Weather at time of sampling: Temp. _____ °C

_____ Clear _____ Snowing
 _____ Partly Cloudy _____ Blowing
 _____ Overcast _____ Freezing
 _____ Raining _____ Thawing

Snow Conditions at Snow Course

_____ Crusted-supports man on skis/snowshoes.
 _____ Breakable crust-breaks under man on skis/snowshoes.
 _____ Snow soft and powdery-not sticky.
 _____ Snow soft and wet-sticky.
 _____ Snow samples obtained easily.
 _____ Snow samples obtained with moderate difficulty.
 _____ Snow samples obtained with extreme difficulty.
 _____ Ice layer on ground. How thick? _____ cm
 _____ Ground frozen under snow.
 _____ Ground not frozen under snow.
 _____ Ground dry under snow.
 _____ Ground damp under snow.
 _____ Ground wet (saturated) under snow.

General Snow Conditions

What elevation is snow-line generally? _____ m
 Is snow melting on north and east slopes? _____
 Is snow melting on south and west slopes? _____
 How many centimetres of fresh snow at snow course? _____ cm
 Is there evidence of snow-slides? _____

Weather conditions of past month
 _____ generally overcast and stormy.
 _____ generally clear and cold
 _____ generally clear and melting.

REMARKS:

contained in the following SOP's (U.S. EPA):

1. EMSL/RTP-SOP-QAD-531, Extracting and Analyzing Dry Deposition Samples, May 14, 1985.
2. EMSL/RTP-SOP-QAD-503, Analysis of Anion Samples by IC. January 30, 1985.

All sample aliquots arrive at a central laboratory in special containers on a weekly basis. SOPs exist for all phases of analysis and quality control. This wilderness area protocol includes the collection and analysis procedures developed by the Illinois State Water Survey and outlined in Peden et al. (1986).

Samples should be analyzed at a central laboratory. To ensure uniform handling, the melting, filtration, and bottling processes should follow strict protocol (Shockey and Taylor 1984). During melting, the overall temperature of the sample should never exceed 4°C. This procedure will minimize any bacterial deterioration of the nutrient constituents. Immediately after thawing at the central laboratory, the samples should be filtered.

Because low, near-detection-limit concentrations of solute are expected in the snowpack from remote regions, extraordinary care must be taken in sampling, processing, and analysis, as well as in collection of many samples, if a valid picture of total deposition is to be obtained. Such standard operating procedures must be developed as part of a quality assurance plan. The procedures for analysis of the melted snow are analogous to those used for precipitation samples.

Measurements made by continuous monitors are collected on a data logger at each site with back-up by strip chart recorder. The logger should be a Campbell Scientific Model CR21X/L or equivalent. The collection of continuous data is designed to: 1) compute accurate averages or sums by regular sampling of the data channel, 2) allow checking of data on a regular basis to spot deviations from expected operation, and 3) retrieve the data efficiently.

Flags will be placed on variables that have yielded less than 200 valid observations for a 60-minute period because this average is considered potentially invalid. Magnetic media will be collected on a weekly basis (or daily by telephone polling if available). Strip charts serve as the final backup if the data logger should fail.

Strip charts will be changed every 2 weeks and archived for referral as needed. Strip charts are necessary if compliance with standard QA/QC procedures are considered essential. The polled data should be examined by experienced personnel to detect any instrument problems and suspect data that need to be checked or validated at the site. The data should be processed at a designated processing center and checked for range validity, rate of change, and other automatic checks programmed into the data archive system. Flags are assigned to suspect data. All flagged data should be examined by an experienced data technician. The technician reviews the magnetic media or strip charts as necessary to validate questionable data. The data are

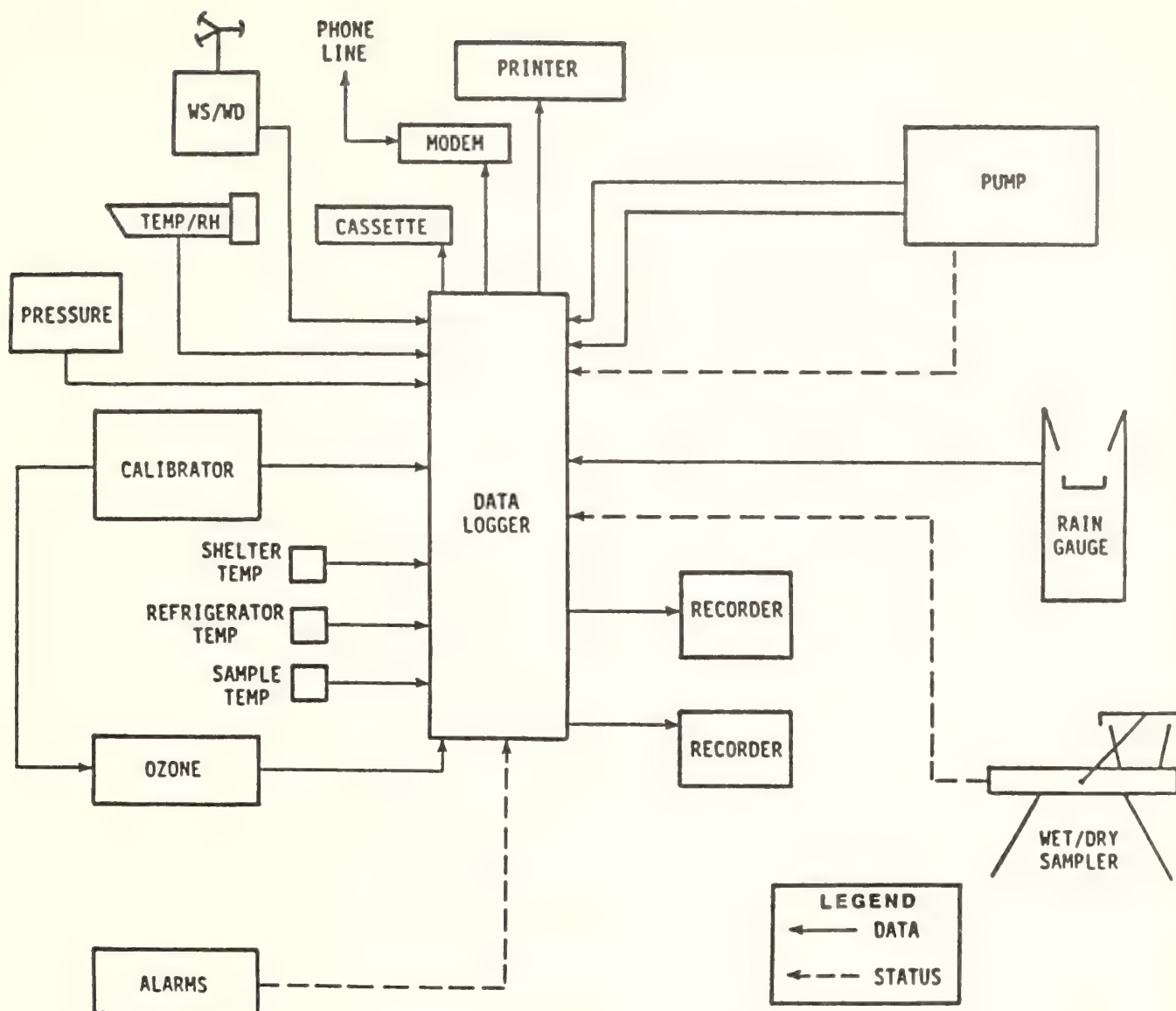


Figure 4.--Schematic of data logging for meteorological and associated measurements.

summarized each month. Quality control is achieved by checking in the field and at the central location. Protocols for QA/QC are available from several field programs.

Quality Assurance

The aerometric, meteorological, precipitation, and snow core data collected by the site personnel should be of a quality consistent with the requirement of impact assessment. Archiving this goal will require a well-conceived quality assurance plan and rigorous adherence to this plan throughout all operational phases of wilderness measurement (NADP 1984b).

Quality assurance can be divided into two types of activities: quality control and quality auditing.

Quality control consists of a set of

mandatory procedures to be followed during the design, collection, and analysis phases of a measurement program. These procedures are designed to insure that the data from the program meet a predetermined set of performance criteria. Quality control activities also provide the information needed to determine the uncertainty in the measurements, i.e., precision and accuracy. Quality control is therefore an ongoing activity performed by the persons actually making the measurements.

The performance of instrumentation and laboratory procedures may be evaluated by comparison with NBS-traceable standards or by the analysis of blind samples. The performance of data processing procedures is tested by independently processing representative sets of measurements by an auditor. Whenever possible, existing QA/QC protocols and SOPs are to be used.

Data Analysis

The monitoring protocol outlined for the wilderness area provides aerometric and precipitation data sets with known accuracy and precision. The accuracy and precision of analytical measurements of air or precipitation samples are evaluated, in principle, in the following manner: 1) accuracy is determined by analyzing EPA and NBS reference samples, unknown reference samples, and spiked samples; 2) precision is determined by analyzing replicated filter or precipitation samples.

The aerometric measurements are reported as concentration in parts per billion (ppb) by volume and in micrograms per cubic meter ($\mu\text{g}/\text{m}^3$), averaged over a time period of seven days. (The protocol is still open as to the sampling mode, i.e., separate day-night samples averaged over one week or one week total average.)

The precipitation measurements (warm season) are reported as concentration in micromoles per liter ($\mu\text{mole}/\text{l}$) averaged over the weekly sampling period. The total precipitation volume accumulated during one week is reported in milliliters (ml). Precipitation amount is recorded separately by the rain gauge as millimeters per day. The snowpack samples are reported as concentration averaged over the entire accumulation time. The total amount of snow accumulated is presented in snow depth, water equivalent, and total volume of water (liters).

From these primary data, one can derive dry and wet deposition data. In addition, the air quality at the boundary of the wilderness area can be established. Air quality within the wilderness area can be estimated by combining the locally measured meteorological parameters with the synoptic scale air flow obtained from standard weather stations.

Concern over the deposition of acidic substances has led to an awareness of limitations in the current ability to monitor dry deposition. At present, relatively few programs are designed to produce dry deposition flux estimates, in contrast to the existence of several networks that produce wet deposition fluxes. The delay in setting up dry deposition monitoring networks is due primarily to the scientific uncertainty of the necessary measurements. No unequivocally accepted method exists for monitoring dry deposition.

Because it is difficult to measure fluxes at the surface itself, dry deposition rates are usually inferred from data obtained in the air above the surface. The critical assumption in this approach is that fluxes measured above the surface are the same as those at the surface, an assumption that depends on the homogeneity of the surroundings.

The deposition velocity, v_d , if known, provides a convenient method for deriving the deposition flux, F , from measurements of concentration in air, C : $F = v_d C$. This calculation is the basis for the inferential or "concentration-monitoring" method. However, the deposition velocity is not fixed for each

pollutant species and surface of interest. In reality, values of v_d are site-specific and time-varying. For this reason, knowledge of the land use and vegetation cover within the wilderness area is essential to associate "appropriate" situation-dependent deposition velocities with the measured, ambient pollutant concentration.

Since the air quality parameters have been measured at another location (at the periphery of the wilderness area), the dry deposition flux as derived in this protocol can only be used as a rough guideline to indicate the influx of pollutants. As a rough guess, the dry deposition fluxes estimated on the basis of this protocol may be accurate only to a factor of two, whereas the concentration values are significantly more precise.

On the other hand, wet deposition and total deposition (snow pack) may be obtained with uncertainties less than 50%, particularly if local precipitation amount is known. Wet deposition is derived as the product of concentration and rainfall amount (warm season). Total deposition accumulated over the cold season is obtained directly from snow depth (water equivalent) and measured concentration of pollutant material in the snow pack.

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Visibility

Visibility (including site visual range, contrast, color, plume blight) in Class I areas is protected under the provisions of the Clean Air Act of 1977, which stipulates that the visibility within Class I areas is not to be degraded and, if possible, is to be brought back to pristine levels. Only visual scenes within Class I area boundaries are protected; "integral vistas" are not protected.

Visibility measurements can be made by several techniques. Since monitoring equipment is not permitted within Forest Service Wilderness boundaries, the Forest Service has adopted the policy of monitoring visibility from locations adjacent to the boundaries. It is assumed that the measurements taken from the nearby site looking into and across the Wilderness are representative of the Class I visual air quality.

A primary goal of visibility monitoring is to quantify how well the image forming information in a vista is transmitted through the atmosphere to an observer some distance away. This requires an understanding of atmospheric extinction (the scattering and absorbing properties of the atmosphere that influence the transmission of light).

Three primary operational electro-optical monitoring techniques are available: integrating nephelometers (Charlson et al. 1967); teleradiometric techniques using natural targets (Malm and Molenaar 1984, Johnson et al. 1985); and transmissometers (Malm et al. 1986, Malm and Tombach 1986). Each method has advantages and disadvantages. For monitoring near wilderness areas where access and manpower are limited and power is generally unavailable, the most successfully applied technique has been photography. Photography has therefore been selected as a practical and economical measurement method.

Transmissometry techniques are currently planned for several Forest Service Wilderness areas as part of the IMPROVE program (Interagency Monitoring of Protected Visual Environments, Joseph et al. 1986). However, current transmissometer systems are experimental and have power, data collection, installation, cost, service, and logistics requirements that make them impractical at most wilderness sites.

Photographic Visibility System

The photographic technique was first proposed by Steffans (1949) and was later refined by Hoffer et al. (1982) and Johnson et al. (1985). Photography offers simplicity and economy in data acquisition with the added advantages of 1) quality assurance of the measurements during data reduction and analysis, and 2) a 35mm slide archive available for future analysis and reference.

The primary electro-optical measurement of target/sky horizon contrast is made by

microdensitometric analysis of the 35mm slides. This technique emulates teleradiometer measurements. The technique is an indirect measurement of the visual air quality because it depends on the film media to accurately depict visual conditions. Sampling is limited to daylight hours.

The color slides can provide the following information:

1. The general condition of the sky and terrain features.
2. The relative color of the sky and terrain features, as well as the presence of layered or uniform haze.
3. A target/sky horizon contrast that is reducible to standard visual range under optimal conditions.
4. Slide archives that provide an easily interpreted and relatively permanent visual record of conditions within the wilderness.

System Components

A primary photographic monitoring system includes the following components:

1. Rugged, reliable 35mm camera body with automatic film winder. The camera's automatic exposure meter must be designed so that it is on only during the actual time of exposure and not continuously operating.
2. 135mm lens with UV filter.
3. Databack capable of imprinting the day and time the exposure was taken on the film.
4. Battery powered programmable timer capable of triggering the camera at least three times per day.
5. The complete system must be able to be housed in a small, stand-alone environmental closure, and operate within the ambient temperature range of -30° to 130° F unattended for at least 10 days.

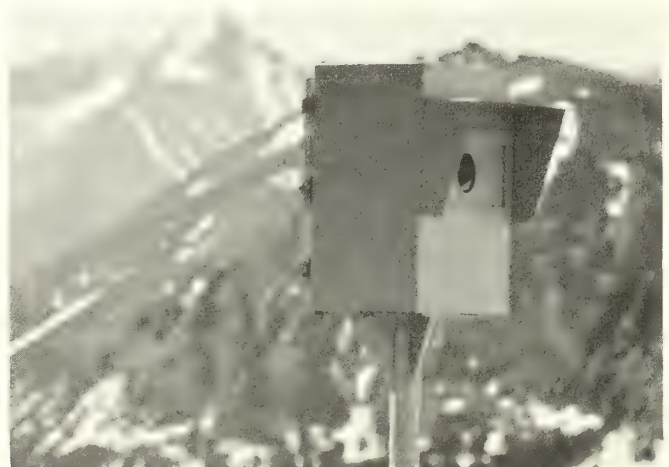


Figure 5.--Field installation of automatic photographic visibility monitoring used at many Forest Service and Park Service sites (photo courtesy of Air Resource Specialists, Inc., Fort Collins, CO)

A commercially available system (from Air Resource Specialists, Inc.) that meets all of the above criteria is shown in figures 5 and 6. Systems are currently operating in over 25 Forest Service sites. A variety of camera configurations can be fabricated to meet specific site requirements. For example, some existing Forest Service sites operate dual camera systems that take two exposures per day and are serviced monthly.

Photographic Siting Criteria

The overall configuration of the monitoring site depends on the characteristics of the site and target. In most cases, the site will be in an undeveloped location with a quality view. The location should be reasonably accessible and secure year-round. The monitoring view should be selected by personnel experienced in photographic exposure techniques and familiar with the practical aspects and limitations of slide microdensitometry. The monitoring site and target should be selected so that as much of the sight path as possible runs through the wilderness.

The view must contain at least one horizon visibility target with as many as possible of the following characteristics:

1. Large--subtend at least 0.1 degree of solid angle (approximately 20% of the size of the full moon.)
2. Easily identifiable on topographic maps of the area.
3. Dark--preferably covered with coniferous vegetation.
4. Distance--preferably in the range of 40% to 60% of the expected standard visual range. General guidelines are: 30 to 70 kilometers in the western U.S.; 10 to 40 kilometers in the eastern U.S.
5. Number of targets--at least one quality target is required; two or three targets at various distances are preferred.
6. Elevation angle--the site and target should be at approximately the same elevation.



Figure 6.--A closeup view of photographic visibility monitoring enclosure (photo courtesy of Air Resource Specialists, Inc.).

The observer-target elevation angle should be within $\pm 1^\circ$.

7. Targets should be located in the center of the camera view finder (center 30% of the slide).

8. For evaluation of regional air quality, the observer-target sight path should not be affected by local sources of visual air pollution.

9. Target should be selected to be as free of snow during the winter months as possible. Standard visual range values cannot be calculated for snow-covered targets.

10. Avoid exceptionally bright or dark foreground objects that would adversely affect the camera's ability to accurately meter the monitoring view.

11. Sun angle--it is best to orient the target to avoid the sun shining directly into the lens.

System and Operation Costs

System and operational costs depend on site and sampling requirements. The approximate equipment cost for a single camera site, fully outfitted to include 35mm camera, 135mm lens, UV filter, databack, programmable timer, batteries, environmental enclosure, internal locks, sunshield, monitoring hardware, mounting post, tripod head, cabling, documentation chart, instruction manuals, and lens cleaning supplies, would be about \$2,100.

Operational costs depend on the sampling frequency and analytical services. An average cost of contracted services that includes all film, film processing, data analysis, reporting, and archiving is \$5,250 per year (3 photographs per day, 365 days per year). For first-time sites, a one-time site initialization charge of approximately \$1,000 is also charged to cover the costs of preparing site specifications and performing inherent contrast analyses. On-site servicing by local personnel to change film and verify system performance is required every 10 days, and on an average amounts to two to three man-weeks per year including travel time.

It is also suggested that sufficient backup equipment be maintained to ensure continuous network operations.

Field Service Procedures

Routine operations and sampling.--Local personnel will serve as the site operators, and will be responsible for the routine operation of the camera systems. Automatic cameras will take three photographs per day at 0900, 1200, and 1500 local time. Kodachrome ASA 25 color slide film will be used. This film was chosen for its fine grain and excellent color reproduction qualities. For consistency, all film will be developed at the Los Angeles Kodak laboratory. Photographs will be taken using the automatic exposure capabilities of the camera.

At many sites, access limits monitoring to snow-free periods. A number of existing Forest Service sites currently operate for limited periods, such as from late June or July through September.

Site visit/servicing protocols.--Film should

be changed every 10 or 11 days, based on three shots per day and 36-exposure film rolls. A site visit by the field operator will generally include the following:

1. General site/system inspection
2. Remove camera; remove and replace film (fill out ID label)
3. Inspect and clean camera lens and box window
4. Check batteries and databack
5. Photograph film documentation board
6. Replace and align camera
7. Check camera and timer settings
8. Complete Visibility Monitoring Status Assessment Sheet

9. Close and lock camera shelter
10. Mail film and Status Assessment Sheet
Detailed protocols and maintenance procedures for camera systems have been applied throughout existing Forest Service networks for several years.

Collection, reduction and analysis of photographic data.--The major steps in the handling of photographic data are summarized in figure 7.

All film collected at the sites must be mailed as soon as possible to a Central Processing Facility. All rolls will be logged and forwarded to Kodak for processing. All returned slides will be identified by a site code and consecutively numbered. Any missing or inconsistent samples will be noted and corrective action taken.

For qualitative analysis, the condition observed on each slide will be assigned an identification code. These codes identify weather conditions, observed hazes or plumes, and visibility target illumination conditions. Appropriate qualitative summaries can be prepared from these codes. For example: In 20 percent of data the visibility target is obscured by clouds; layered hazes were observed on 30 percent of 0900 observations.

The basis for quantitative analysis is the measurement of the contrast (in the 550 nm wavelength) between and sky and selected terrain horizon features. This contrast measurement can be reduced to yield a standard visual range value in kilometers. This quantitative measurement is related directly to the site path between the observer and the target. Only the conditions within the path are quantified in this type of analysis.

Reporting.--The results of qualitative and quantitative analyses can be reported in a variety of formats. Most results will be summarized by monitoring season. Example report products could include:

- Site specifications summary, including: site and target constants data, and data collection statistics summaries.
- Qualitative slide condition code summary and statistics.
- Slide and scene contrast listing for each slide.
- SVR listings for each day, time, and target as well as 0900, 1200, and 1500 daily geometric mean SVR.

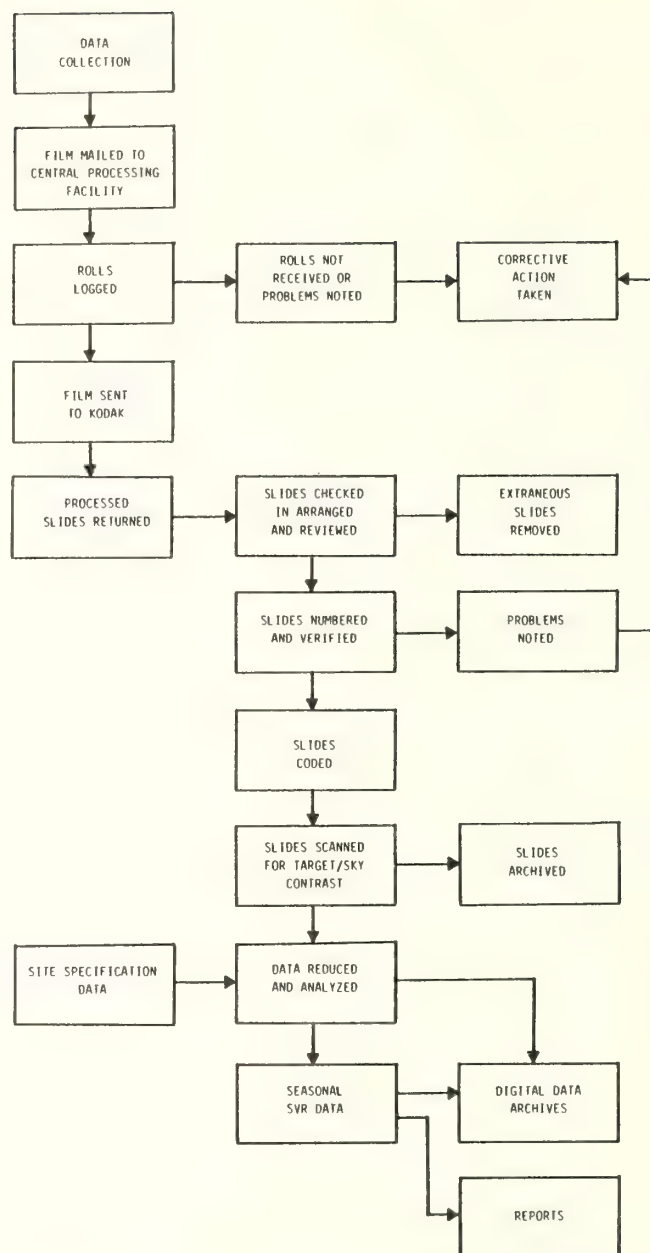


Figure 7.--Steps in the handling of photographic data.

- Monthly plots of daily maximum, minimum, and geometric mean SVR.
- Seasonal standard visual range summaries, statistics, and plots.

All original slides will be archived by site in a Central Processing Facility. All qualitative and quantitative results will be archived in both digital and hard copy formats.

Quality assurance.--All applied procedures will follow fully documented quality assurance procedures. Procedures have been established and operationally applied to account for: film quality; film handling, processing, archiving, and storage; camera operation; scanning; data handling; analysis; and reporting.

Transmissometer Measurement System

Transmissometers are a direct method of measuring atmospheric extinction. Transmissometers consist of a constant-output light source transmitter and a computer-controlled photometer receiver. The two individually housed components must be separated by a line of sight distance of approximately .5 to 10 km, depending on the average extinction coefficient. The irradiance at the 550 nm wavelength from the transmitter can be determined by measuring the light loss from the transmitter to the receiver. Data are collected on logging systems and strip chart recorders.

Several transmissometer installations are planned for Forest Service wildernesses as part of the IMPROVE program. These initial experimental installations will provide further insights into the practical application of transmissometry for monitoring visual air quality in wildernesses. The initial experimental systems are costly to purchase and install. Power can be provided by solar panels at some sunny locations; line power will be required at the receiver at many sites. Both ends of the transmissometer must be serviced weekly by field operators. Trained technicians must visit the site to replace components and calibrate at least every six months.

Siting transmissometers near wildernesses may be difficult since neither end of the system can be installed in the wilderness. Sight paths must generally be elevated to reduce the effect of turbulence caused by surface heating on the light beam.

The advantages of the transmissometer are that the system directly measures atmospheric extinction, both day and night. Continuous measurements can be averaged for selected sampling periods. Disadvantages include high cost, power requirements, sheltering, installation, and servicing logistics. In general, it is recommended that camera systems be operated along with the transmissometer to correlate measured extinction with visual conditions, and as a quality assurance reference.

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Soils and Geology

Purpose

Soil functions in the ecosystem in roles that are important to the productivity and diversity of the terrestrial and aquatic biota. In addition, it has a self-contained biota, and is an efficient trap or collection system for many atmospheric contaminants. A careful description and a set of quantitative measurements of the soil are essential to estimating the sensitivity or stability of the ecosystem, and to determining its response to atmospheric input. The goals of this section are to provide a guide in selecting areas to sample, and to suggest methods for use in the field and laboratory to accomplish the following:

1. Characterize the soil-geologic resource, and evaluate its sensitivity to internal change and its ability to buffer the aquatic system. This information will be used to assist in evaluating the susceptibility or vulnerability of the soils to change due to changes in air quality.

2. Determine the present condition of soils in terms of pH, nutrient ions, metal load, etc. as a reference value to measure future changes against. This information will be used to monitor the system for evidence of change via repeated measurements.

One important factor that must be considered is response time; while soil and geologic features significantly influence the aquatic and terrestrial biological systems, their response to air quality change is likely to be slow and difficult to measure in a time span of a few years.

List of Measures

The assumed sensitivity of high elevation systems is partially due to the expectation that much of the area may be bare rock, the geologic material is little weathered or perhaps resistant to weathering, and the soils are coarse and shallow, providing little buffer capacity. A reconnaissance survey of the geology is necessary to focus the limited resources for sampling on sites that are most likely to be susceptible to change. The soil physical and chemical properties recommended for measurement here should not be considered limiting. Other measures will be appropriate when the particular area or air source suggests them, but those included in table 8 will be adequate and reasonable in cost for most areas. If advanced analytical techniques for soil extracts are used, the content of additional metals, for example, might be available at little or no extra cost.

Useful measurements such as bulk density and permeability should be taken where soils contain few stones and allow the extraction of intact volumes with coring devices. Such measurements may be prohibited by equipment needs or excessive time requirements in most alpine areas. While

Table 8.—Measurements for characterizing soils and geology.

Attributes	Methods	Reference no. ³
Soil description Horizons, depth, field pH, texture, structure, color, consistence	Pit at plot edge and extent checked by borings	1
Mineralogy sand, silt clay	(Mineral soil horizons) Microscopic examination X-ray diffraction	2,2a
Laboratory analyses carbon	Combustion to CO ₂	3
LOI (ash)	Wt. after combustion @ 550 C	3
pH	1:1 H ₂ O and 1.1N KCl	4
exchangeable ions	1N NH ₄ Ac extract.	5
Ca	Atomic absorption	
Mg	Atomic absorption	
K	Atomic absorption	
Al	Atomic absorption	
Na	Atomic absorption	
Cation exchange capacity	Saturation with Ba repl. with Mg	6
Exchangeable acidity or titratable acidity	BaCl-triethanolamine extract.	7,7a
Percent base saturation	Calculated from measures above	
Extractable SO ₄	Water and phosphate extract. ion chromatography	8
Total N in O horizon	Micro-Kjeldahl	9
Total S in O horizon	Leco combustion to SO ₂	10
Sulfate retained	Equilibrium with sulfate at 2 and 20 mg/l, ion chromatography	11
Metal content	HCl extractable	12
Pb	Atomic absorption, flameless	
Cd	Atomic absorption, flameless	
Zn	Atomic absorption, flameless	
Ni	Atomic absorption, flameless	
Cu	Atomic absorption, flameless	
Inorganic carbonates ¹	CO ₂ release, HCl treatment	13
Intact soil cores ²		
bulk density	volume and mass	14
pore space	calculated from b.d.	14
permeability	tempe cell	14a

¹The test for amount of carbonates in the soil material can be deleted if soil pH in water is neutral or acid.

²Should be taken where soil is relatively stone-free and intact cores can be obtained with reasonable effort with simple cans or coring device.

³References identified in table 10.

these additional physical measurements are useful in characterization, they are not of the highest priority since they are not likely to be sensitive indicators of atmospheric changes. Bulk density concentrations in soil are to be converted to mass-per-area basis.

Table 8 lists the measures to be used in both the initial characterization and in the periodic sampling. The soil description, mineralogy, particle size analysis, and reconnaissance geologic survey would not be repeated. Table 9 lists the detection levels and laboratory precision of the measurements.

Table 9.—Proposed detection limits and laboratory analytical precision goals.

Attributes	Units	Detection limits	Precision goals
Nitrogen	g/kg	1.0	5%
Carbon	g/kg	1.0	5%
Loss on ignition	g/kg	1.0	5%
pH	pH units	—	±0.1
Exch. calcium	cmole/kg	0.02	5%
Exch. magnesium	cmole/kg	0.02	5%
Exch. potassium	cmole/kg	0.02	5%
Exch. aluminum	cmole/kg	0.02	5%
Exch. sodium	cmole/kg	0.02	5%
Cation exch. cap.	cmole(+)/kg	0.1	5%
Exch. acidity	cmole/kg	0.1	5%
Sulfate	mg/kg	0.5	5%
Sulfur	mg/kg	0.5	5%
Lead	mg/kg	0.1	5%
Cadmium	mg/kg	0.1	5%
Zinc	mg/kg	0.1	5%
Nickel	mg/kg	0.1	5%
Copper	mg/kg	0.1	5%
Other metals	mg/kg	0.1	5%
Bulk density	g/cm ²	0.1	5%
Pore space	ml/ml	0.01	5%
Permeability	cm/hr	0.1	5%
Carbonate	g/kg	1.0	5%

Requirements

Initial characterization of the geology and soils, including writing descriptions, requires the services of two highly trained individuals--a soil scientist and a geologist--both with field experience. Subsequent field sampling of soils can be accomplished by technicians. Approximately one day per site is required for the geologist and soil scientist, assuming the goal is to characterize an area of less than 3 km². Subsequent periodic sampling can be accomplished in one day per site.

Field equipment to be transported into the area is listed below. All equipment needed for the soil and geologic characterization and sampling is transportable on one pack animal.

Soil auger
Sampling tube
Spade
Knife
Topographic maps and aerial photographs
Field pH kit
Soil color book
Notebook
Measuring tape
Polypropylene sample bottles (1 L)
Cloth and plastic bags
Compass
Abney level

Table 10.—References for analytical techniques.

Reference no.	Citation
1	Soil Survey Staff. 1981. Soil Survey Manual. USDA--SCS, Agriculture Handbook No. 430, U.S. Government Printing Office, Washington, DC. Chapter 4.
2	Robarge, W.P. and I. Fernandez. 1986. Laboratory Analytical Methods Manual (draft). U.S. EPA, Washington, DC. pp. 102-105.
2a	Klute, A. 1986. Methods of Soil Analysis, Part 1. 2nd Edition, ASA Monograph No. 9, American Soc. Agronomy, Madison, WI. pp. 185-186, 336-356.
3	Page, A.L., R.H. Miller, and D.R. Keeney. 1982. Methods of Soil Analysis, Part 2. ASA Monograph No. 9 (2nd ed.), American Soc. Agronomy, Madison, WI. pp. 539-552. (Also see Robarge and Fernandez, pp. 179-180.)
4	Page, A.L., R.H. Miller, and D.R. Keeney. 1982. pp. 208-209. Robarge, W.P. and I. Fernandez. 1986. pp. 130-134.
5	Robarge, W.P. and I. Fernandez. 1986. pp. 130-140. Page, A.L., R.H. Miller, and D.R. Keeney. 1982. pp. 159-164.
6	Page, A.L., R.H. Miller, and D.R. Keeney. 1982. pp. 149-157.
7	Page, A.L., R.H. Miller, and D.R. Keeney. 1982. pp. 159-164.
7a	Robarge, W.P. and I. Fernandez. 1986. pp. 141-148.
8	Robarge, W.P. and I. Fernandez. 1986. pp. 159-164. Johnson, D.W. and G.S. Henderson. 1979. Sulfate adsorption and sulfur fractions in a highly weathered soil under a mixed deciduous forest. Soil Sci. 128:34-40.
9	Page, A.L., R.H. Miller, and D.R. Keeney. 1982. pp. 595-622.
10	Page, A.L., R.H. Miller, and D.R. Keeney. 1982. pp. 501-534. Robarge, W.P. and I. Fernandez. 1986. pp. 130-134.
11	Johnson, D.W. and G.S. Henderson. 1979. Robarge, W.P. and I. Fernandez. 1986. Blume, L.J. 1985. Statement of Work, National Acid Deposition Soil Survey. Chemical and Physical Characteristics of Soils. IFB No WA 85-566 EMSL, U.S. EPA, Las Vegas, NV.
12	Robarge, W.P. and I. Fernandez. 1986. pp. 149-153. Page, A.L., R.H. Miller, and D.R. Keeney. 1982. pp. 323-334, 347-362.
13	Page, A.L., R.H. Miller, and D.R. Keeney. 1982. pp. 188-191.
14	Klute, A. 1986. pp. 363-667.
14a	Klute, A. 1986. pp. 694-700.

Soil coring device with removable rings
Frame, 20 cm X 20 cm
Camera
Ground cloth
Rock hammer

Field Procedure

Site Selection Process and Geologic Characterization

The site selection process will be the responsibility of the land manager, and quite specific for each region. We suggest a hierarchical approach working from very large land areas, such as the entire wilderness area, down to selecting the landscape units (small watersheds, for example) that will be

characterized and sampled. All of the available information from numerous disciplines should be integrated in the landscape unit selection process. Information on geology, soils, aquatics, vegetation, and general knowledge of the area, including public concerns and proximity to known or potential contamination sources, will be useful.

After landscape units are selected, plots, lakes, and streams are selected for more intensive characterization and long-term monitoring. Each watershed or landscape unit selected is mapped for bedrock and surficial geology on a reconnaissance scale. The soils are mapped at the same scale and differentiated at family or subgroup level, or mapped by soil associations if recognized soil series are available. Since these mapping procedures are somewhat subjective and require a trained scientist following established procedures common to the discipline, they are not included here.

Sampling Strategy

Conceptually, a few carefully chosen plots can be considered representative of sensitive areas, even though they may not be truly representative of the entire area of concern. A few plots thoroughly characterized for soil and vegetative properties can be monitored for change more easily and result in higher probability of detecting adverse impact than a sampling scheme directed at whole watersheds or whole wilderness areas.

Selection of plots begins with a map survey (using aerial photographs) and the selection of specific landscape units thought to be the most sensitive. The sampling plots themselves should be representative of major soil-geologic-vegetative types within the landscape unit chosen. Whenever possible, the sample plots should be coordinated with those for aquatics and vegetation. In addition, the choice of location should also consider proximity to pollution sources, public concerns, and area coverage.

Location of plots.--Due to size, diversity, and spatial variability, permanent plots will be established in selected geology-soil-vegetation associations within major watersheds surrounding lakes and/or streams that are being sampled. This strategy will provide the opportunity for more precise characterization of small, representative segments of the area under study, rather than attempting to characterize current conditions throughout the area. Because of the lack of any prior classification scheme in which "associations" in these regions are recognized, on-the-spot classifications and descriptions will usually be necessary.

Size of plots.--Alpine mosaics, whether recognized as patches or as changes along gradients, are usually finer grained than even a tenth of a hectare. Therefore, plots will by necessity often include more than one vegetation "type" in order to provide adequate size for repeated sampling without destruction of the site. Although some flexibility in size is necessary to accommodate differences in fineness

and complexity of the soils-geologic-vegetative types, we recommend a target size of 1000 m².

Sample Location, Number, and Frequency

The reconnaissance geologic survey maps and aerial photographs will be used on-site to select plots for detailed characterization. These plots will be limited in number, depending on the size and complexity of the watershed or other geologic unit selected. The plots should be the same as those used in the vegetation studies. Plots should be permanently marked at four corners with flush markers located on photographs by reference to prominent landmarks.

For the initial characterization, a single soil pit is dug at the edge of the plot for detailed descriptions, and approximately 1-liter samples are collected, horizon by horizon, to a depth of 1.5 meters or to a limiting layer. Borings (which minimize disturbance) are taken around the periphery of the plot to ensure that the pit is representative of most of the soil over the plot.

Because one goal is to measure temporal trends, the emphasis is on surface soil samples. Deep samples are needed for complete characterization of the site. Within each permanent plot, 12 samples each of the 0 horizon(s), if present, and top 2 cm of surface mineral horizon are taken at each sample interval.

Samples taken to detect changes should be collected on a 5- to 10-year cycle. More frequent sampling is unlikely to show changes, even in severely contaminated areas.

Sample Collection Procedure

Sample pH should be determined immediately in the field by the dye technique (table 8). Organic horizons can be placed directly into bottles or plastic bags after separation of the mineral soil. The 0 horizon samples should be collected from within a known surface area by cutting around the inside of a 20 cm X 20 cm frame. Moist mineral soil samples gently crushed and passed through a 2 mm stainless steel screen should be placed in 1 L polypropylene bottles for transport. Bottles should be permanently numbered. A record of bottle number, sample location, depth, date, and remarks should be kept and as much information as possible also recorded on the bottles. An estimate of percentage of material above 2 mm (that screened out) should be recorded. Samples of the coarse material should be taken in cloth bags for mineralogical analysis. Initial samples taken from the pit should include undisturbed core samples, representative of each horizon, for bulk density, pore space, and permeability tests.

Field Storage and Handling

Soil samples for pH, extractable sulfate, and nitrogen should be maintained as moist and cool as possible until they reach the laboratory, where the sample can be split. An aliquot for the above analyses is stored at 4°C and the remainder is air-dried for physical and chemical

analyses. Air-dried samples can be stored indefinitely at room temperature.

Hydrologic Sampling

In remote areas, the sampling of springs and seeps offers the best approach to sampling soil water. Sites are permanently marked for sequential sampling, and subjected to analyses prescribed for lakes and streams. Alternatively, tube lysimeters could be installed for periodic sampling if groundwater measurements are essential, but the procedures are not described here.

Laboratory Analysis

Only the initial samples will be subjected to

bulk density, permeability, mineralogical, and textural classification.

The characterization samples and the surface horizons collected repeatedly should be analyzed for the chemical properties shown in table 8. The methods to be used are found in the references cited in table 8 and listed in table 10.

Support Needs

Because the soil sampling should support the vegetation analyses and the aquatic characterization, their locations must be coordinated.

Aquatic Chemistry

Purpose

The objective of this section is to provide guidance for determining current chemical characteristics of surface waters in alpine and subalpine wilderness areas. The proposed guidelines are essentially limited to sample acquisition, stabilization, and analysis.

Development of a detailed sampling program for application in all potential study areas is not feasible. Area-specific information, including the expected nature of potential impacts, and the spatial and temporal variation in measurable response parameters, must be considered. Although design issues cannot be pre-specified, in general a two-stage strategy is recommended for determining current chemical characteristics of surface waters. Stage I would determine the presence and spatial distribution of sensitive surface water systems. The level of effort required at Stage I will depend on the amount of existing information. Stage II would then involve the selection of sensitive system(s) for more intensive study and longer-term monitoring. If information on historical rates of deposition is required, sediment coring could be a component of Stage II, and would require additional protocols.

The following protocol is proposed as a practical approach to obtaining an initial characterization of current chemistry of lakes and streams in remote high-elevation wilderness areas. In conjunction with a sampling design appropriate to local conditions, these attributes and this sampling and analysis methodology should meet a Stage I objective of establishing the range and distribution of chemically differing aquatic systems. A sufficiently reliable basis would be provided for establishing classes of aquatic systems according to sensitivity of response types. Depending upon further

definition of objectives, a more rigorous sampling and analysis protocol could be implemented for the Stage II sampling program to identify temporal variation and trends.

Land managers may view the methods of investigation described within this protocol as general guidance rather than detailed requirements. Methods actually employed would depend upon the potential AQRV impacts, the resources available for the task of characterization, and the specific management objectives.

List of Measures

Major Ions in Water (including Al)

Table 11 provides a general list of measurements important for characterizing surface water composition. The list includes the major mineral species commonly present in low ionic strength surface waters, and the basic parameters associated with nutrient status and biological productivity. The list of measurements may be considered optimal, though not all-inclusive, depending upon case-specific conditions. Some constituents, including aluminum fractions, dissolved organic carbon, fluoride, and ammonium, are commonly present at very low concentrations. After confirmation of low concentrations, these measurements could be deleted, or obtained on a less frequent basis than other constituents. Dissolved oxygen and transparency measurements would only be obtained when mid-lake sampling is conducted.

Table 11 also lists the recommended methods of sample analysis. Accuracy and precision goals are listed in table 12. Sample container and preservation requirements are listed in table 13. Sample holding times are listed in table 14. Specific analytical procedures are provided by reference to the National Surface Water Survey

Table 11.—Measurements required for characterizing water quality conditions.

Attributes	Methods
Alkalinity	Gran's method
Aluminum (labile and total)	Atomic absorption spectrophotometry (graphite furnace)
Ammonium	Standard indophenol blue technique
Calcium	Atomic absorption spectrophotometry or ICP
Chloride	Ion chromatography
Chlorophyll a ¹	Methanol extraction/fluorescence
Dissolved organic carbon	Infrared spectrophotometry
Fluoride	Ion-selective electrode and meter
Magnesium	Atomic absorption spectrophotometry or ICP
Nitrate	Ion chromatography
pH	pH electrode with expanded-range pH meter (closed system)
Phosphate	Standard molybdenum blue technique
Potassium	Atomic absorption spectrophotometry
Silica	Standard molybdenum blue technique or ICP
Sodium	Atomic absorption spectrophotometry
Sulfate	Ion chromatography
Conductance	Conductivity cell and meter
Dissolved oxygen	Dissolved-oxygen meter
Transparency	Secchi disk

¹Chlorophyll a determinations are included to support the aquatic biology protocol in the following section.

(NSWS), a regional-scale survey of stream and lake chemistry conducted by the U.S. EPA. The NSWS provides the most credible and well-documented protocol for determination of chemistry in natural, low ionic strength waters. This project includes a Western Lake Survey conducted in cooperation with the Forest Service. The results of this work should provide an improved perspective on sampling and analysis methods as well as on the degree of precision and accuracy attainable.

Of specific interest is the comparative study of pH measurements, including the development and use of a closed system pH determination. Preliminary results favor this method based on precision and accuracy levels. Inclusion of this method in the proposed protocol would eliminate the need for in situ pH determinations, which would greatly expedite the sample collection process. The NSWS is ongoing, with important methodological findings still emerging. The methods proposed may not fully reflect the current information status; the proposed protocol should be considered tentative and subject to modification as results of the NSWS and other current studies supporting methods assessment become available.

The recommendation for use of NSWS methods should be viewed as guidance rather than prescribed requirements. Any alternate methods employed should attain equivalent levels of

Table 12.—Proposed detection limits and analytical precision and accuracy.

Attributes	Units	Detection limits	Relative standard deviation ¹	Accuracy maximum bias
Alkalinity	ueq/l	5	10%	10%
Aluminum, total	mg/l	0.005	20%	20%
Aluminum, extractable	mg/l	0.005	20%	20%
Ammonium	mg/l	0.01	5%	10%
Calcium	mg/l	0.01	5%	10%
Chloride	mg/l	0.01	5%	10%
Chlorophyll a ²	ug/l	0.02	5%	10%
Dissolved organic carbon	mg/l	0.1	10%	10%
Dissolved oxygen	mg/l	-	5%	5%
Fluoride	mg/l	0.005	5%	10%
Magnesium	mg/l	0.01	5%	10%
Nitrate	mg/l	0.005	10%	10%
pH				
Field	pH units	-	-	-
Lab	pH units	-	-	±0.1 pH
Phosphate, total dissolved	mg/l	0.002	20%	20%
Potassium	mg/l	0.01	5%	10%
Silica	mg/l	0.05	5%	10%
Sodium	mg/l	0.01	5%	10%
Sulfate	mg/l	0.05	5%	10%
Conductance at 25° C	uS/cm	-	1%	5%

¹RSD at concentrations 10X above detection limits.

²Chlorophyll a determinations are included to support the aquatic biology protocol in the following section.

precision and accuracy, or be otherwise justified. Detailed documentation of any methods used should be considered a necessity.

Trace Metals in Sediments

Trace metals in sediments can provide historical deposition records. Studies in Rocky Mountain National Park and in the Wind River Range indicate a history of atmospheric input of some heavy metals (most notably Pb) over a +100-year period. Collecting this record is a viable research goal to determine the history of the input of atmospheric pollutants that are preserved (not necessarily in proportion to atmospheric flux) in lake sediment or peat. (There are probably few ombrotrophic bogs suitable for such studies.) Briefly, we suggest the following in conjunction with Stage II sampling if information is needed on historical deposition rates.

1. Coring of lake sediment from selected lakes.

2. Abbreviated analysis of sediments to establish approximate chronology and compare pre-1800 to modern chemical-biological characteristics.

3. Sample intervals: 1-2, 5-6, 10-11, 15-16, 20-21, 25-26, 30-31, 35-36, 40-41 cm.

4. Chemical parameters: ²¹⁰Pb activity,

Table 13.--Recommended sampling aliquots, containers, and preservation.

1 (1000 ml) LDPE bottle	Container and preservation		
	2 (125 ml) LDPE bottle	3 sealed 60-ml syringe	4 sealed 60-ml syringe
Kept cold in dark	pH < 2 with H ₂ SO ₄	Kept cold in dark	Kept cold in dark
----- Attributes -----			
Cl ⁻	DOC	pH ³	Al ¹
F ⁻	NH ₄ ⁺		
SO ₄ ²⁻			
NO ₃ ⁻			
SiO ₂			
Ca ²⁺			
Mg ²⁺			
K ⁺			
Na ⁺			
Total P			
Total Al			
Al ²			
Alkalinity			
Spec. conductance			
pH ²			

NOTE: As stated in text, concentrations of DOC, Al, and NH₄ are usually low and may not require routine analysis. In that case, only two aliquots, (1) and (3), would be collected.

pH² = laboratory pH, open system measurement, obtained at lab temperature with an open system.

pH³ = closed system pH.

Al¹ = laboratory extraction of closed system sample for organic and inorganic fractions.

Al² = total Al.

Chlorophyll a: Field extracts are obtained according to Holm-Hansen and Riemann (1978).

H₂O and organic content, major metals (Cd, Mg, K, Na, Al, Fe, Mn), trace metals (Pb, Zn, Cd, Cu, B), polycyclic aromatic hydrocarbons, charcoal, and soot.

5. Biological parameters: diatoms, chrysophytes, and pollen.

It will also be possible to evaluate the flux of anthropogenic material (atmospheric pollutants) to the sediments.

Coring of lake sediment is difficult, and is even more difficult given the constraints imposed in wilderness areas. If sediment coring is deemed necessary, a well-developed protocol will be necessary.

Trace Metals in Water

We recommend that only labile and total aluminum be determined in the surveys because aluminum is biologically important, it is very sensitive to changes in pH, and natural levels can be measured with fair precision and accuracy.

We do not recommend that other metals be measured because none have been identified as having effects on biotic systems at natural levels, natural variability is high and therefore trends will be difficult to discern, and trace metals are difficult (and expensive) to collect and analyze at natural levels.

Table 14.--Analysis time frame.

On site	Same day	One week	Four weeks
pH ¹	pH ²	pH ³	SO ₄ ²⁻
DO		Al ¹	NO ₃ ^{-*}
		DOC	SiO ₂
		NO ₃	Al ²
		Specific conductance	NH ₄ ⁺
			Ca ²⁺
			Mg ²⁺
			Na ⁺
			K ⁺
			Cl ⁻
			F ⁻
			Total PO ₄ ³⁻
			Alkalinity

pH Options: 1. In situ pH, open system measurement obtained at field temperature.

2. Laboratory pH, open system measurement, obtained at lab temperature.

3. Closed system pH.

Al¹ Laboratory extraction of closed system sample for organic and inorganic fractions.

Al² Total Al.

NO₃* The NSW holding time is 1 week, but some evidence indicates stability for 2-4 weeks if maintained at 4° C in the dark.

Chlorophyll a: Maximum of three weeks - see Holm-Hansen and Riemann (1978).

Requirements

Manpower

The level of effort required to collect the recommended samples has two components: 1) traveling to the sampling site, and 2) sampling the water and sediment. The amount of time required to get to the sampling sites will be site-specific and cannot be prescribed except to say that enough travel time should be allocated so that field operators can perform careful work at the sampling site.

The amount of time required to take the water samples is approximately 0.5 day, although individual sites may require longer. To take sediment cores, an additional 0.5 - 1 day is necessary.

Equipment

Backpacks

Sampling containers for each location: 1

1000-ml LDPE (low

density polyethylene) bottle, 1 125-ml LDPE bottle, and 2 60-ml

syringes

pH and conductivity meters

Ice and coolers for samples

Raft when taking mid-lake samples

Van Dorn bottle, dissolved oxygen meter, and Secchi disk when taking mid-lake samples

Field Procedures

Sampling Strategy

Stage I in a two-stage sampling strategy would be conducted to determine the distribution of sensitive lake and stream systems. The level of effort required at this stage will depend upon the value of existing data. Existing data would be adequate if determined sufficient to identify the most sensitive landscape units and place the watersheds in sensitivity classes. Synoptic survey data should be obtained that reflect the spatial scale and distribution of response controlling landscapes. Records of existing surface water chemistry, as well as maps of surficial materials (soils and geology) and vegetation, should be employed in identifying landscape units and in determining additional data collection needs. Even where surface waters can be lumped into general sensitivity classifications, a more detailed survey focused on individual classes may be useful for identifying the most sensitive class members.

Stage II would require selection of the most sensitive class, or classes, of lakes and streams for monitoring and more intensive study. Ideally, one small, well-defined watershed would provide an excellent study area for measurements of aquatic chemistry and biology, and also vegetation and soils. These measurements are easier to perform, interpret, and subsequently monitor when they are made within the same known watershed.

Location of Sampling Sites at Lakes and Streams

If mid-lake samples are to be taken, lakes should be sampled 1.5 meters below their surface in the middle of the lake. Samples of the outlet and a major inlet also should be sampled at a location with appreciable water flow (i.e., no stagnant pools).

Streams should be sampled mid-stream in areas of appreciable flow.

Number of Water Samples and Frequency of Sampling

Two to four aliquots should be taken at each site, depending upon the suite of analyses. Each aliquot has its own preservation and treatment protocol (table 13). This sampling protocol generally is adopted from the NSW. Our protocol differs from the NSW protocol in that it does not recommend filtering (because of contamination problems and the lack of large amounts of suspended particulates in the high elevation surface waters) and sampling treatment is minimized. This recommendation does not preclude filtration warranted by site conditions (e.g., high turbidity) or emphasis on a specific parameter (e.g., concentration of dissolved phosphate).

At least 10 percent of all sampling and analysis should be done in duplicate to provide an indication of the uncertainty associated with the sampling and analysis procedures. Additional quality assurance protocols should be used as described in the quality assurance plans developed for the NSW (see Drouse et al. 1986). At a minimum, quality assurance should

include analysis of sampling replicates, blanks, and NBS traceable reference standards.

Sample frequency should include 3-4 samples per year taken between early spring and early autumn. The exact date of the first sample will depend upon field conditions.

Water Sample Collection Procedures

The lake and stream water sampling procedures of the NSW (1986) should be used. In general, lake and stream samples should be collected with LDPE sampling containers that have been acid-washed and copiously rinsed with deionized water. At the sampling site, the bottles and the caps should be rinsed 3 times with the lake or stream water before taking the sample. The syringes should be rinsed three times prior to sample collection. Samples should be placed on ice immediately after collection.

Field Measurements

We recommend that specific conductance measurements be taken each time samples are collected. Dissolved oxygen and transparency would be measured on site when mid-lake sampling is conducted. In situ pH measurement (pH_i in table 11) can be taken if the closed system measurement (pH³) method is not used. We recommend closed system pH measurement because of the low precision associated with in situ open system measurements. If in situ pH¹ is measured in lieu of the closed system pH³, we recommend that an open system lab measurement (pH⁻) also be made.

Water Sample Storage and Transport

Immediately after collection, the samples should be packed in an insulated container with a refrigerant, and thereafter maintained in the dark at approximately 4°C until analyzed.

Laboratory Sample Analyses

The recommended methods for analysis of water samples are listed in table 11. (Note preceding statement concerning use of alternate methods.) These methods are described by Hillman et al. (1986). The appropriate units of measure are listed in table 12.

Support Needs

No biological measurements are required to support the chemical measurements.

In addition to the physical measurements already mentioned (e.g., transparency), additional physical measurements are water temperature and, in the case of streams, water flow.

Data Analysis

Data analysis that would be required in addition to standard statistical analyses to determine data quality, depend on the objective of the study and how well it is realized in the sampling design and, thus, cannot be prescribed here.

Aquatic Biology

Purpose

The primary objective of monitoring aquatic biota in wilderness areas is to provide information on the status of sensitive biological communities over time. Man-induced change or lack of change can then be inferred from data patterns. This general goal must be considered within the context of limited monitoring resources (constraints of time, money, access to sampling sites) which, for example, may preclude the study of seasonal biological dynamics. Cause-and-effect relationships between anthropogenic disturbances and biological responses also cannot be delineated (except for catastrophic change) in complex ecological systems by monitoring alone. Moreover, the sensitivities of specific aquatic biota to different anthropogenic stresses generally are poorly known in subalpine and alpine regions. Consequently, the monitoring activities described here represent our best approximation of a minimal array of sensitive components that, if monitored with reasonable intensity and frequency, will provide an estimate of the health of aquatic communities in remote wilderness regions.

Although sampling error undoubtedly will be high (i.e., high variance among replicate and time series data), we have little alternative to accepting high error short of simple presence/absence surveys or no monitoring at all. Although present monitoring methods may be crude, it is obvious that the alternatives are undesirable from a resource management perspective.

The biological components that constitute a minimal set for detecting change in alpine and subalpine waters are Chlorophyll a, salmonid fisheries, and macroinvertebrates. Chlorophyll a (tables 11 and 12, Aquatic Chemistry) is the best readily measurable attribute of phytoplankton biomass (primary producers) related to the trophic status of surface waters, which may be stimulated (fertilized) or reduced by atmospheric deposition. Macroinvertebrates and salmonid fish are sensitive to many types of anthropogenic disturbances; are not typically ephemeral in a given lake or stream (although specific life-cycle periods are ephemeral); can be quantitatively monitored by routine field practices; and in the case of fish, are highly valued components of wilderness surface waters.

Monitoring of other aspects of lower trophic levels (such as phytoplankton and zooplankton community structure) presently is not recommended as part of the minimal set for the following reasons:

1. these lower trophic levels have high natural variability, both seasonally and year-to-year;
2. we do not understand the complex of factors that drives the shifts in community

structure or biomass during early stages of anthropogenic disturbance (e.g., lake and stream acidification) especially in low-productivity systems;

3. they have low or unknown sensitivity to change during early stages of anthropogenic disturbance; and

4. archiving of biological samples for future analysis is not likely to be feasible.

However, anthropogenic stress affects a broad variety of aquatic organisms. The wilderness resource manager should consider expanding the minimal monitoring program suggested in this protocol as resources permit. Studies that may be particularly useful include studies of attached algae, macrophytes, zooplankton, and amphibians (particularly salamanders).

As previously noted, these protocols are intended to be general guidelines rather than detailed field manuals or research directives. Although we recognize that alternative monitoring approaches such as remote sensing of the trophic status of wilderness lakes have great potential to increase the accuracy and geographic extent of the monitoring effort, such developmental approaches are not discussed here.

Salmonid Fish

The following protocol is constrained by limitations of access, time, manpower, and transport of equipment inherent in sampling of high-elevation lakes in remote wilderness regions. Such limitations dictate that only a small set of basic data be collected to characterize fish stocks. Further assumptions used to develop this protocol are described in the following paragraphs.

The general objective of this protocol is to correlate independent fishery variables with changes in surface water quality. However, quantitative assessment of fishery stocks in remote lakes for long-term trend analysis is not well developed. Most monitoring of high-elevation fisheries has been biased toward general management goals that do not require a high degree of accuracy or precision of technique. For example, the efficiency of sampling effort using specific gear is a function of fish species, standing stock, seasonal behavior, habitat, and morphometric features of lakes, and is not quantified for high-elevation salmonid fisheries. Little guidance on the quantification of alpine salmonid fish stocks can be derived from existing data. Consequently, collection of unbiased fishery data in wilderness lakes is unlikely (Thornton et al. 1986).

Because the availability of sampling gear at each lake will be limited, sampling for target fish species will be emphasized. This may preclude complete characterization of the fish community in some lakes. However, many alpine and subalpine lakes did not historically contain

fish, and existing fish populations have been established by stocking.

Therefore, many high-altitude fisheries contain only one or two species of introduced salmonids. For example, only a few cutthroat populations were found historically in the high-elevation lakes of the Wind River Mountains in Wyoming. Other fish species associated with oligotrophic conditions are not commonly found. For example, sculpins, suckers, and dace are not found in high-elevation lakes in Wyoming due to high gradient streams, although sculpins are occasionally found in mid-elevation lakes. Speckled dace and long-nose suckers are found in some alpine lakes in Colorado but their occurrence is not common; both of these species have probably been introduced.

The lakes selected for long-term monitoring should, if possible, also be used for chemical monitoring (see Aquatic Chemistry section). However, monitored lakes must be capable of sustaining fisheries over periods of many years (e.g., probability of winter kill must be low) and the lakes must not exhibit a high degree of heterogeneity of fish habitats (e.g., selected lakes should be relatively circular and not contain coves) which tend to develop sub-populations of fish. Lake morphometry should be relatively uniform, conducive to random dispersal of active fish populations. Harvest by angling should be insignificant compared to natural sources of mortality, and be relatively constant year to year. The potential for over-harvesting by fishermen must be considered during lake selection.

Ideally, lake fisheries that are monitored should be sustained by natural reproduction because early life stages of salmonids are very sensitive to changes in water quality. This may be an impractical constraint, however, because many lake fisheries in alpine wilderness regions are maintained by periodic stocking. In addition, the availability of spawning habitat has been found to be positively correlated with population strength and size of individual fish in wilderness lakes (Hudelson et al. 1980).

Salmonid fisheries are assumed to be of primary interest. Such fisheries are to be sampled once during a sampling year over a 2-3 day period using equipment that can be transported to the site. The field crew should consist of 2-3 individuals using an inflatable raft. A requirement for non-destructive sampling in wilderness lakes will be adhered to as much as possible, but complete elimination of sampling mortality is difficult.

Experience has shown that absolute measures of fish stocks are difficult and time-consuming in the alpine (e.g., mark-recapture techniques require at least one week of sampling). Thus, the specific objectives here are to quantify relative indices of fishery status. These include (beyond presence of a specific fishery) the following:

1. catch per unit effort (CPUE),
2. population age structure,
3. condition factors,
4. growth and mortality rates, and
5. absence of year classes or weak year classes.

Field Sampling

Sampling design.--Collection of representative, random samples of individuals from a fish stock optimally should be based on a stratified random sampling design where strata represent different habitat types. In alpine lakes that have restricted sampling area (due to steep morphometry, boulder fields, or other morphometric features), site-specific judgement on net placement may be based on experience with collecting mobile salmonids if experience dictates that a representative sample of fish from the total stock will be collected.

Sampling frequency.--It is generally recommended that the frequency of fish sampling be related to the potential rate of change of surface water chemistry (Lambou et al. 1985). For intensively monitored lakes where close observation of fishery status is desired in the event that such lakes undergo rapid change (e.g., dilute headwater lakes), fish should be sampled at 1- to 2-year intervals. For lakes not expected to exhibit rapid chemical change (e.g., larger or less dilute subalpine lakes), fish should be sampled at 3- to 4-year intervals (Lambou et al. 1985). Fish should be sampled once during mid to late summer so that young-of-year may be observed. This time will vary from late July to late August, depending upon whether fish spawn in fall or spring.

Sampling intensity.--Sampling intensity should involve both minimal sampling effort and minimal sample sizes. Minimal sampling effort should be expended at each monitored lake according to the recommended number of net sets for lakes of given sizes (see Net Placement). Minimal sample size should be collected according to the following protocols.

For each monitored species, 100-150 fish should be collected, with 150 being preferred. Some field experience suggests, however, that as few as 30 captured individuals may be adequate to characterize fisheries with limited stock size (Remmick 1984). Other recommendations include sampling at least 10 fish per 2 cm size length over the size range of maximum accuracy for individual fish statistics (see discussion below). Lambou et al. (1985) recommend that at least 60 fish evenly distributed across size classes be measured for developing fishery statistics (see also Thornton et al. 1986).

It should also be noted that stressed fish populations contain the fewest individuals and require the greatest effort to achieve population estimates of known variance.

Field Procedures

Sampling gear.--Because collecting unbiased fishery data is difficult, more than one type of sampling gear should be used. However, experience has shown that monofilament gill nets are effective in collecting most fish species found in remote Rocky Mountain lakes (e.g., Hudelson et al. 1980) and are easily transported. Trap nets are presently being designed that are more portable than previously available (e.g., modified Alaska trap net; ALSC 1985). Such nets may become useful in the future to supplement gill netting, although portable trap nets did not prove effective for surveying

fish stocks in small Maine lakes (Haines et al. 1985).

Swedish gill nets (standard 150 ft length, 6 ft depth with 5 panels of 1/2, 3/4, 1, 1 1/2 inch bar mesh) should be used because they are especially effective in capturing mobile salmonid species. These nets are capable of capturing fish as small as 7-8 cm total length. Thus, the gill netting should be effective on age I fish and older, but should not catch young-of-year.

Net placement.--Analysis of trends in fishery status based upon results of gill netting will only be as reliable as the reproducibility of sampling technique for each monitored lake. Location of nets, orientation along the bottom in relation to shoreline, time of placement and collection, and season of placement must be standardized for each lake. Because lake sampling programs will be site specific, standardization must be within a given lake and not necessarily between lakes.

Fish captured by nets operated in a similar manner and time each sampling year should provide reasonably comparable estimates of population characteristics (Hubert 1983). Close adherence to standard collection procedures for each lake will minimize total variance in catch statistics due to unknown or uncontrollable biotic and abiotic factors.

Each lake has a unique morphometry, and net placement must be carefully considered according to lake characteristics and target species. Generally, gill nets set along the bottom in shallow waters not exceeding 5-7 m depth will capture a representative sample of the total fish stock if crepuscular activity periods are sampled. Salmonids in alpine lakes in the Rocky Mountain region are typically found in relatively shallow waters, and in general are closely associated with the benthos as the primary food resource (e.g., golden trout are found in close proximity to sediment). Nets should be placed perpendicular to the shoreline in shallow water or at 45° angles in deep water, with the small mesh nearest shoreline. If the initial sampling effort yields few or no fish, the sampling stations should be moved and the sampling effort repeated.

A rough guideline for number of nets to use is as follows:

<u>Lake size</u>	<u>Number of 150 ft. Swedish gill nets required</u>
Less than 10 acres	1
10-25 acres	2
25-50 acres	3
50-100 acres	4
Each additional 100 acres	add 1 net

Three gill nets set in different habitat may be the maximum number effectively operated by a field crew of 2-3 persons.

Sampling mortality should be minimized in wilderness lakes, especially in those with relatively small fish populations. Thus, gill nets should be deployed by midday in

high-elevation lakes where foraging by salmonids is more or less continuous. These nets should be tended every 1 1/2 to 2 hours to minimize capture mortality. The nets should be run until after dusk to bracket one crepuscular activity period. If fish are abundant, and some sampling mortality is acceptable, one net set over night may be useful to sample larger, night-feeding individuals. Overnight sets where the dusk (one hour before sunset) and dawn (one hour after sunrise) activity periods are bracketed generally will capture a representative sample of fish, but such long sets may produce mortalities above 50% in captured fish.

Fish processing.--Fish in unproductive high-elevation lakes generally grow very slowly in the older age classes due to food limitation. Generally, rapid growth occurs in such lakes only to approximately 20-25 cm in total length. Thus, older fish are more difficult to age accurately by scale readings. Obtaining accurate weights in the field on fish smaller than 12-15 cm also is difficult due to variations in water content and from wind effects on weighing devices. Additionally, the more numerous individuals in the younger age classes place large demands on a lake ecosystem to provide habitat and food. Therefore, it is appropriate to obtain weight-length measurements for all fish captured, unless sub-sampling is required due to large numbers of individuals captured. But fish in the 12-25 cm total length range only should be used to determine the population parameters discussed below.

Handling time should be minimized once fish are removed from the net. Fish should be kept in a live-car attached to the side of the raft during handling, and be released as soon after capture and measurement as possible. Handling mortality should be recorded if observed. Procedures for reducing handling mortality have been reviewed by Stickney (1983).

Fish collected should be carefully removed from the gill net (using a small polished hook to minimize damage to fish and technician), identified to species, measured to nearest mm, weighed to nearest gm (by volume displacement for fish less than 50 gm and by spring scale for fish greater than 50 gm), and scale samples taken (on left side just posterior to and below dorsal fin and above the lateral line).

Recording of field data.--Field data recording should be standardized, and include the following:

- lake;
- sampling date;
- gear type;
- net location, shoreline orientation, depth, placement time, and collection intervals;
- species, weight (gm), total length (cm), and location of scale collection site for each individual fish collected;
- observations of parasites, wounds, deformities, or other abnormalities; and
- capture mortality and injury.

Lake temperature at sampling location and other

pertinent chemical condition information such as dissolved oxygen or pH should be recorded on field sheets, if measured.

Additional fish surveys.--A reconnaissance-level, qualitative assessment of reproductive success can be made by looking for juvenile fish in shallow habitat and in shoreline cover. Small hand seines and dip nets may be used to find young-of-year, but capture success may be limited. Small baited hardware cloth minnow traps have not proved effective in capturing young-of-year salmonids (T. Haines, personal communication). Alternatively, trapping of drifting fry in outlet streams during sampling for macroinvertebrate drift may be possible.

Laboratory Procedures

Use of scales to age individuals from wild salmonid populations during the early rapid growth phases of ages I-IV is the most accurate, non-destructive technique available. However, aging by scale analysis is not as accurate for stocked fish due to possible interruption of growth in the period immediately following stocking. Stocking may produce a growth check similar to an annulus. Fall-spawning species such as lake trout produce a better annulus during age 0 in comparison to species that spawn in late spring such as cutthroat and golden trout. The latter sometimes do not get a good scale growth before the first winter, and produce an indistinct first annulus.

Technicians should be carefully trained using scales from the monitored species that are from fish of known age and comparable growth environment. Random recounting of approximately 5% of fish scales by a second trained technician is appropriate as a quality assurance check. An 80-90% comparison of scale readings between two technicians typically is good (Thornton et al. 1986). If possible, fish scales should be aged by the same personnel over the life of the monitoring effort to minimize error.

Supporting Data

As noted above, the fisheries monitored should be in lakes whose water chemistry is also being monitored. Better resolution of ongoing environmental change or stability will result from such integrated studies.

Data Analysis

Catch Per Unit Effort (CPUE).--Catch per unit effort is a relative measure of population strength. Theoretically, it should be linearly proportional to the abundance of fish stock: catch = capture efficiency x fishing effort x fish abundance. However, capture by passive fishing techniques is a function of fish movement. Consequently, CPUE is not dependent fully on stock size (Hubert 1983), and has frequently been found to be non-linear (Bannerot and Austin 1983). Fishery biologists have long recognized variability in CPUE results from problems of gear efficiency due to interacting biotic and abiotic factors that affect fish movement.

Common problems with CPUE studies include spatial correlation among sampling units, inverse

non-linear relationships between capture efficiency and population abundance, and skewed frequency distributions for CPUE with zero catch being most frequently recorded. (See review in Thornton et al. 1986). The high variability among units of sampling effort (catch per net hour or per net night) may result in poor statistical resolution of stock means or patterns of population fluctuations (Bannerot and Austin 1983, Thornton et al. 1986). CPUE will therefore provide only semi-quantitative estimates of fish abundance.

Transformed catch data and the relative frequency of zero CPUE have been demonstrated to be the best indicators of population abundance. Catch data should be reported as catch per net hour or per net night (means and variances) for each species captured (Bannerot and Austin 1983).

Population age structure.--Evaluation of population age structure depends on obtaining a representative sample of the overall population. As noted above, passive fishing techniques using gill nets tend to produce skewed data, with older and younger fish being less efficiently captured. Additionally, aging of fish by reading of scales is most accurate in the age I-IV classes for alpine salmonid fisheries. Thus, age-frequency data for y-o-y and older age classes generally will be qualitative. Age frequency distribution within the I-IV age classes will be most quantitative.

Captured fish should be aged by scale readings using standard techniques (Lagler 1956, Jerald 1983). As with CPUE, age frequency data may be transformed to achieve independence of variance and mean.

Condition factors.--Weight and length are quantitative attributes of individual fish that can be easily measured in the field. Relationships between weights and lengths indicate the relative abundance of food and relative quality of habitat for growth. Condition factors for each age class I-IV should be calculated. For example,

$$CF = (W \times 10^5) / L^3$$

where: CF is condition factor

W is weight in pounds

L is total length in inches

Condition factors are typically reported in English units. For comparison with existing data from State game and fish departments, it probably is best to continue using English units (Remmick 1984.)

Relative condition factors or analysis of covariance among weight/length data for specific subgroups captured (for example, grouped according to same species, sex, year-class, and physiological condition relative to spawning) also may be used to assess the general growth environment (Anderson and Gutreuter 1983; W. Nelson, Colorado Div. of Fish and Wildlife, personal communication).

Growth and mortality rates.--If sampling has been random among age classes, determination of growth and mortality characteristics will reveal important characteristics of the fish stock for a particular lake. The dependent variables most

commonly related to water and habitat quality include average annual growth increment, instantaneous growth rate, average length of a given age-class, and instantaneous age-class mortality. Again, age classes I-IV should be used to provide the most accurate calculations.

The variable stocking rates of different age-classes in some wilderness lakes will affect accuracy when estimating fish mortality from catch data. Thus, the mathematical structure used to estimate mortality will depend upon the specific conditions related to annual recruitment (Everhardt and Youngs 1981). For those lake fisheries not sustained by natural reproduction, knowledge of stocking rates (species, numbers, sizes, dates) should be obtained from appropriate fishery management groups. Adjustment of catch data by weighting according to stocking records should follow general recommendations in Everhardt and Youngs (1981). If stocked lakes are extensively monitored, marking of each stocked year-class is feasible and should be considered to improve the accuracy of population parameter estimates.

Average annual growth increment between growth intervals of 1-2 cm can be determined by back-calculation techniques using length at age i , determined by scale analysis (Lagler 1956, Whitney and Carlander 1956, Carlander 1981). Fish growth rates also should be calculated using length-weight regression assuming allometric growth: $W = aL^b$, where a and b are growth coefficients.

Instantaneous growth rate is calculated as the difference between natural logarithms of weight for consecutive age groups (Everhardt and Youngs 1981). If annual fish surveys are conducted, instantaneous age-class mortality (Z) may be calculated from the slope of the regression of age versus frequency:

$N_i = N_{i-1} e^{-Z}$ where N_i is number of individuals captured of i th age for a particular year-class.

Missing or weak year classes.--Observations of missing or weak year classes in a fish stock may indicate changing habitat conditions or density-independent mortality, resulting primarily from weather. Missing or weak year classes are common occurrences in wild fish populations; gear inefficiency and poor age determinations preclude accurate estimates of older age class strength. Thus, for a given lake, the occurrence of missing or weak year classes in catch data is neither a definitive characteristic of the fishery, nor necessarily an indicator of anthropogenic change related to atmospheric deposition. However, patterns of similar age-frequency distributions (number and sequence of low frequency year classes) among monitored lakes in the same region may be indicative of regional conditions or change (Thornton et al. 1986).

Detection Goals

Presently, there are no standard references that quantitatively define detection goals for changes in the indices discussed for high-elevation salmonid fisheries. Comparable analyses of fishery data from remote lakes using

stock assessment by gill netting are being conducted by the U.S. Environmental Protection Agency as part of the National Surface Water Survey. Results of these analyses, which are expected in several years, will help define realistic detection goals for some salmonid species with restricted stock sizes and for limited sampling.

It must be stressed that, due to inherent variability in gear efficiency between lakes, fishery statistics cannot be compared between different monitored lakes, but only within a given lake over a sequence of years.

Based upon reasonable age determination of 1- to 4- year-old fish, changes may be detected in relative growth and mortality indices on the order of 20-50% for specific year-classes, but achievement of these goals is uncertain. Estimates of changes in absolute characteristics of an alpine fish stock will be less precise. Changes in the neighborhood of only 2-3x will be considered valid on the basis of reasonable adherence to assumptions of random sampling of fish stock and independence of variances and means. Estimates of age will be particularly troublesome. In general, aging by scale reading produces estimates of higher mortality rates than actually are present due to poor aging of older fish (on the order of 10-20% too high; Jerald 1983). Precision of age determinations should be estimated according to Chang (1982).

Additional protocols for sampling fish may be found in Armour et al. (1983) and from the EPA National Surface Water Survey (Fabrizio et al. 1987, Hagley et al. 1987).

Macroinvertebrates

Aquatic macroinvertebrates are animals without backbones that live in streams and lakes, and are big enough to be seen without a microscope when in advanced stages of development. They have been observed to be sensitive to low pH conditions in lakes and streams (Napier and Hummon 1976; Parsons 1968; Warner 1973; Nichols and Bulow 1973; Tomkiewicz and Dunson 1977; Witters et al. 1984; Havas and Hutchinson 1982; Bell 1971; Hall and Ide 1987; Hall and Likens 1985; Singer 1981, 1984). Tolerances of aquatic invertebrate species vary according to their specific anatomical, behavioral, and physiological adaptations (Hynes 1972). Since some macroinvertebrates are more tolerant to acid conditions than others (Parsons 1968, Warner 1973, Bell 1971, Robak 1974, Eilers et al. 1984, Hall and Likens 1980, Sutcliffe and Carrick 1973), they may be used as a functional part of the warning system established to monitor possible effects of air pollution in high-elevation ecosystems.

The following equipment and procedures are being used by federal and State agencies in western regions of the United States, and may provide a common basis for collection of macroinvertebrate data.

Equipment

Modified Surber net (see fig. 8)
Standard 8" diam. full height 250 micron mesh
Tyler sieve

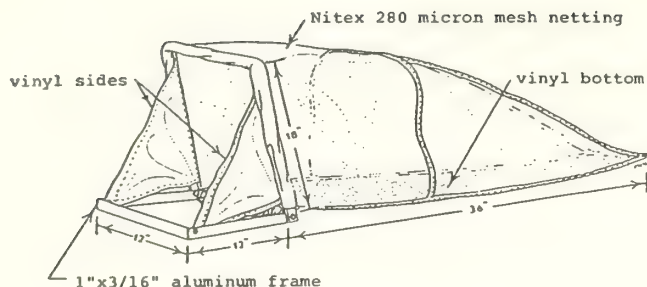


Figure 8.--Modified Surber sampler for use in macroinvertebrate sample collection (from USDA 1985).

8 oz., wide-mouth plastic bottles with strip of masking tape attached for identification data
 Preserving solution: ethyl alcohol plus one cup 10% formalin per gallon of 70% alcohol
 Hip boots
 Saturated salt-water solution
 Two aluminum bread pans
 Waterproof gloves (scuba diving or rubber electrical types recommended)
 Laundry pen (waterproof marker)
 Long-handled 250 micron mesh kick net
 White plastic tray--2.5" x 10" x 12"
 Fine-pointed forceps

Sampling Station and Site Selection

Stations should be established in the inlet and outlet streams of the lake ecosystem to be monitored. In a literature review, Eilers et al. (1984) observed that, with few exceptions, taxa were found in lakes at lower pH values than were taxa in the same order or family in streams. This was mainly because species in streams may experience more short-term pH depression. The sampling station should be in a riffle area having unimbedded rubble substrate (3-12" rocks) if possible. If rubble substrate is not found, whatever substrate is present in the riffle should be sampled. Most of the macroinvertebrate species present will be found in the rubble substrate, which has been called the "breadbasket" of the stream (Bell 1969, Cairns et al. 1971, Hart and Brusven 1976, Pennak 1977).

Number and Frequency of Sampling

Quantifying stream benthic macroinvertebrates is difficult due to the spatial and temporal variation in species abundance (Needham and Usinger, 1956). As a minimum, three random samples should be taken at each station. Ideally, sites should be sampled with as many samples as possible. Following the recommendations of Elliott (1977), enough samples should be taken such that the standard error is equal to or less than 20 percent of the mean. The needed number of samples should be established for each site for each sampling

season. Under ideal conditions with good access, samples should be taken at least monthly. Year-to-year variation in benthic community composition requires that a site should be monitored for several years.

Modified Surber Net Samples

The modified Surber square foot sample net is recommended for use, because it performs better than alternative sampling devices. The 3-ft-long net and 18-in-high upper frame (fig. 8) reduces the backwash problem often experienced with the original Surber net (USDA 1985).

Sampling Procedure

Streams.--The foot-square modified Surber frame is placed over the gravel-rubble substrate in the stream with the net downstream. As the rocks within the frame are scrubbed, the macroinvertebrates are carried into the net by the flowing water. The substrate underlying the gravel-rubble is also stirred to a depth of 3-4 in (7-10 cm), if possible.

After the water drains from the net, the net is inverted into an aluminum pan containing a saturated salt-water solution. As the salt water is poured into a second pan, the organic materials thus floated are caught in a 250-micron sieve. The salt water is then poured back into the first pan, the contents again vigorously stirred, and the floating materials and specimens are poured for a second time into the sieve. The sample may require sieving two, three, or more times. It is imperative that the pan material be inspected carefully so that non-floating benthos are hand picked and collected. Clams, snails, and cased caddisflies will not float and must be hand picked and added to the sample. Large clams will also not float into the net, and should be sampled from within the Surber frame by hand.

The sample in the sieve is then washed from the sieve pan into the sample bottle with an alcohol solution. Enough alcohol should be added to the sample bottle to cover the sample.

Lakes.--Macroinvertebrate sampling within a lake should include qualitative lake-shore samples for sensitive indicator mayfly, stonefly, caddisfly, and amphipod species. These samples can generally be taken with a long-handled kick net used in a sweeping motion through vegetation or over the lake bottom substrate.

Portions of the net contents can be placed in a white tray with a small amount of water in the bottom for detection and removal of invertebrate fauna with forceps. If the net contains plant materials, put more water in the tray and vigorously wash the plants in the tray. The water and its contents are poured into the 250 micron sieve and then transferred to the sample bottle. The sample data on the bottle should include the words "Qualitative Lake Sample".

Identification of Taxa Collected

The samples collected should be sent for identification by qualified persons. Taxa should be keyed to the highest taxon possible: family, genus, or species, depending on the group. Voucher collections should be maintained and identifications should be checked and verified.

Once the identity and number of individuals in each sample are known, a variety of analysis methods are available.

Data Evaluations

The resultant data (numbers of individuals of each taxon per sample) may be analyzed by a number of methods. Analysis may include the use of indicator species, community composition, synthetic "biotic indices," biomass, abundance, species richness, species diversity, and functional group analysis. The aim is to quantify existing conditions and identify and interpret changes in the stream benthic community. No one method will suffice. It is most important that the data be collected properly with adequate sampling and accurate taxonomic determinations. The method of analysis is not as important as the data quality itself.

Helpful guidelines for sampling and data analysis of stream benthos can be found in Platts et al. (1983). Sources of materials, and an extensive taxonomic literature review of insects, can be found in Merritt and Cummins (1978). Pennak (1978) provides a scholarly guide to the identification of fresh-water invertebrates and Hynes' (1972) tome remains a classic introduction to the ecology of streams. A comprehensive review of statistical methods can be found in Elliott (1977) and a review of the use of indices is found in Washington (1984).

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Plants

Purpose

These guidelines have been prepared to assist the Federal Land Manager (FLM) in designing a measurement program capable of determining current, and monitoring future, responses of vegetation to atmospheric pollution. They are general guidelines rather than specific methods. They are flexible, and guide the FLM in the development of a program suitable for a specific permit and wilderness area.

These guidelines are built on the ongoing programs of several regulatory agencies that assess the effects of pollution on native plants (see Bennett 1984, 1985), but they represent a new synthesis and approach to the problem. The guidelines are based on the acceptance of the principle that changes should be detected in "the most sensitive part of the ecosystem." They are presented as the most efficient and parsimonious steps to make decisions involving present or future effects of atmospheric pollutants.

A primary goal is to obtain measurements of plant air quality related values (AQRVs) within a short period (one growing season), which can be used in the permitting process. However, if funding and the management policy of the Class I area under consideration allow, a secondary goal would be to establish subsequent trends and changes via long-term measurements.

Constraints and Philosophy of Approach

Biological AQRVs worthy of measurement are inherently more difficult to identify than abiotic AQRVs. Further, the significance of their measured value as an indicator of air quality is often ambiguous. The following points provide the background for this comment:

1. No finite list equivalent to that of criteria pollutants exists for organisms and communities.
2. Because of the lack of adequate controls and experimental design, any field observation or sampling will lead only to correlations and inference, not to an established cause and effect of a pollutant on a biological AQRV unless chronic levels of pollution are present.
3. There are no known functional attributes that respond only to specific changes in air quality. The majority, if not all, functional attributes also will be affected by several pollutants and by natural environmental factors.

Synergism will occur between the various controlling factors. Further, some symptoms may have more than one cause, including those other than pollution.

4. Species and individuals vary in their response to environmental stress because of genetic or ecotypic variability. Again, interactions can complicate the picture. For example, stresses can be mitigated or amplified by temporal patterns of the plants or by involvement with pathogenic organisms.

5. Even the functional attributes that may be reasonably related to changes in air quality are poorly described and quantified. Furthermore, even if the dose-response experiments have been done, extension to the field is tenuous. An overall ignorance of the norm makes many attributes, especially physiological ones, of little value.

Measurements in these western high-elevation and montane Class I areas present further difficulties because of the following:

1. These areas tend to be large, inaccessible, diverse, and spatially heterogeneous.
2. The air quality history or current status may be poorly known.
3. The effects of air quality on the native plants, communities, or biotic systems are not fully known.

The protocol has two key elements. The first is the decision to deal with the population level of the plant system rather than higher attributes of the ecosystem. The second key element is the flexibility and general nature of these protocols, which do not provide exact sampling and measurement schemes. Plants, rather than vegetation, provide the operational perspective, which focuses on the presence and performance (health) of individual plant species and their populations, rather than on attributes of vegetation, communities, or ecosystems. The scope of measurement is further reduced by the restriction only to known sensitive taxa and their sensitive organismic systems. The complexity of higher-order ecological units such as community and ecosystems and the difficulty of measuring change in these units, provide ample reason for a population perspective to take precedence over a vegetational or total system perspective.

Nonvascular plants such as mosses and lichens

are considered because of their known sensitivity to air pollution and their established usefulness as indicators. Algae, bacteria, and fungi are not included because they would require special methods that would be beyond any realistic budget for the task. The flexibility of the protocols is justified on the basis that unique programs have to be designed by the FLM and contributing experts to meet the unique characteristics of each permit, each area, and each flora.

There are two parts to the protocols: 1) a flow diagram or decision tree with text explaining the step-by-step process for designing a specific program, and 2) some general guidelines for sampling and analysis procedures. Although the decision regarding permit denial or approval is beyond the scope of these protocols, the position of the permitting decision process is shown in the flow diagram.

Protocol Design

The flow diagram in figure 9 shows the data sets required at the start of the design process, and the decisions necessary to design a measurement program. The required data are shown in lettered boxes, and the processes and decisions, here called steps, in numbered boxes.

A number of data sets are required to decide what, when, and where to measure the flora. These may be available in the literature or specific archives pertaining to the Class I land under consideration. If not available, they should be compiled by the FLM. Available information seldom will be adequate, and preparation of this information will be a mandate and prescription for collection. These compilations may require assistance from experts. The data sets required for each Class I area are described in the sequence of the lettered boxes of figure 9. This protocol is demanding of time and effort; there are no short cuts.

Floristic List

A complete list of vascular plants, lichens, and mosses is needed. This list should show for each species a commonness rating (abundant, frequent, rare) and distributional information (habitat, soil preferences, vegetation associations). Fairly good lists of vascular plants are available for many Class I areas. If these are not available, local floras, herbarium collections, and consultation with local systematic botanists can supply fairly complete lists that include estimates of commonness. Available lists of lichens and mosses are rarely available, and their compilation would not be easy without field surveys by specialists. Distributional information seldom may be pre-compiled but can usually be derived from such sources as floras, plant ecology dissertations, and plant community descriptions from similar nearby regions. This list is meant as a guide in the selection of taxa to be studied, and not as a definitive list against which future losses can be detected.

Land Cover Map

A map of land cover units at a scale between 12,00 and 100,000 would be satisfactory. The land cover units should be based primarily on vegetation assemblages. Each vegetation unit should be described by species content and abundance, and may be additionally defined on the basis of other attributes such as geology, soil, and habitat. Maps of species distribution, if available, would be particularly useful, especially for a rare species whose distribution is difficult to interpret from a vegetation map.

Adequate land cover and/or vegetation maps will only be available for a few areas. Forest inventory maps, soil surveys, and geology maps may be more readily available and may provide background data for land cover maps. Most Class I areas will have reasonable aerial photo coverage, and a skilled aerial photo interpreter, with the help of a local plant ecologist, can produce adequate land cover maps overlaid on USGS topographic maps (1:24,000 or 1:63,360). The comprehensive method of Kuchler (1967) is recommended. The description of vegetation in terms of its composition is critical to the proposed protocol. According to the Kuchler method, this information is gathered as the groundtruth of the map is verified and revised.

Relative Sensitivity Tables

A fundamental assumption of monitoring air pollution effects on plants is that not all species are sensitive to a given pollutant. Therefore, candidate test species must be sensitive to a given pollutant. Furthermore, we agree with Cairns (1986) that there will also be no single reliable most sensitive indicator species for specific pollutants. Therefore, several test species must be selected. Lists of relative sensitivity of plants to specific pollutants may be found in the literature (Applied Science Associates 1976, Davis and Wilhour 1976). The EPA Criteria Documents for each pollutant are a useful source of lists. National experts are useful contributors of information at this point. When information is not available for the actual species on the study area, related taxa or growth-forms (which often, but not always, have similar sensitivities to a pollutant) might be considered.

Air Quality Information

This is required to identify the probable pollutants of concern. Sources of these data will be any previous monitoring, the direct monitoring provided as part of the total protocol (Atmospheric Environment Section of this report), and from the permit application itself. The most desirable data set would contain temporal and spatial distribution of pollutants, and also the frequency concentrations of each pollutant over the area. Atmospheric modeling is often the best source of this distributional information. Research is ongoing on species sensitivity.

List of Responsive Attributes

It is necessary to measure only those

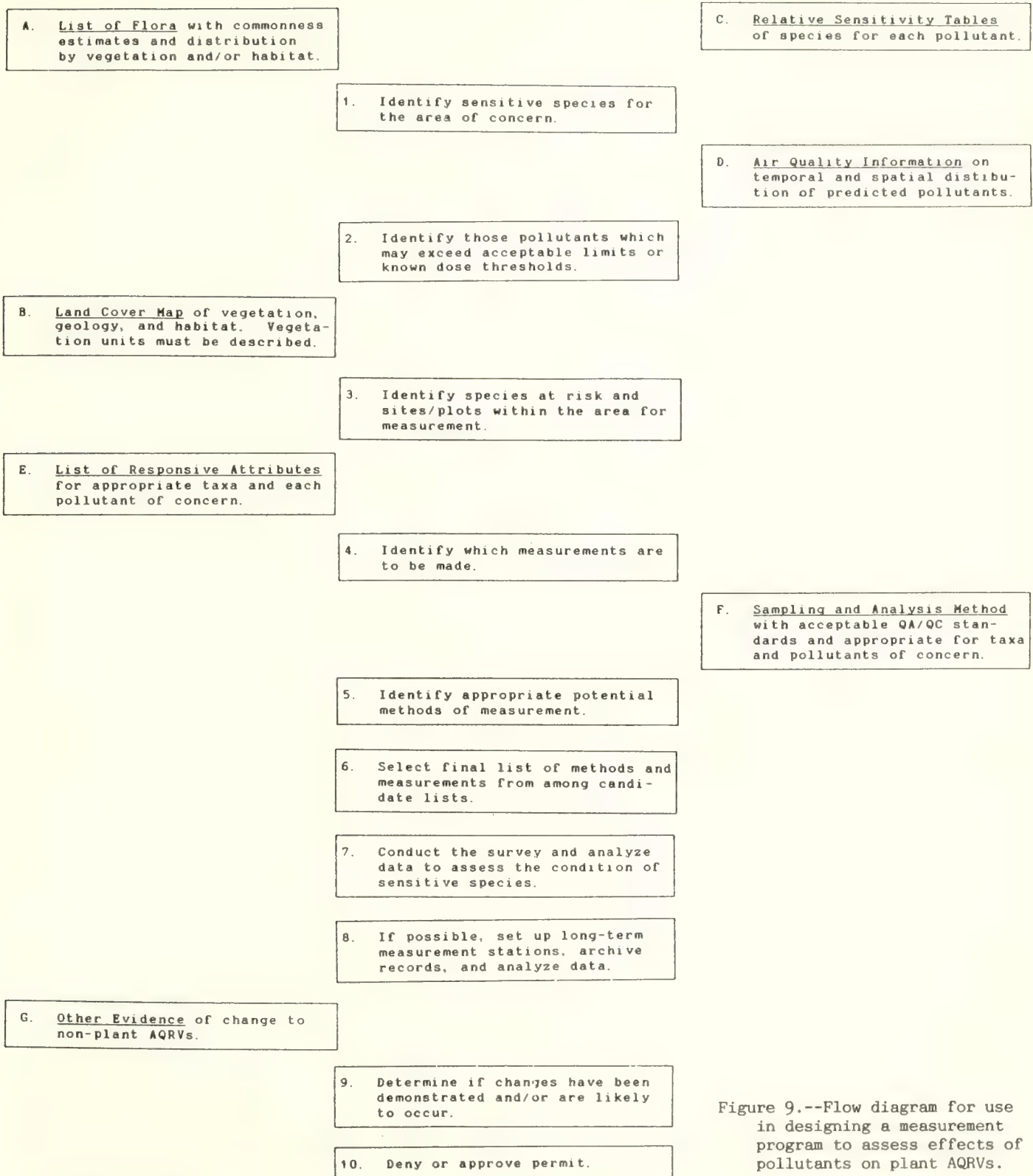


Figure 9.--Flow diagram for use in designing a measurement program to assess effects of pollutants on plant AQRVs.

attributes of sensitive species that clearly show diagnostic responses to pollutants. Injury atlases illustrating damage and stress symptoms are a good source of clues as to appropriate attributes to measure; for example, Jacobson and Hill (1970), U.S. Forest Service (1973), Malhotra

and Blauel (1980), and Thompson, et al. (1984). Table 15 illustrates the type of information required for each pollutant of concern.

Sampling and Analysis Procedures

For each species and attribute, there must be

Table 15.—Examples of the kind of measurement and methods required for the detection of changes in atmospheric pollutants.

Pollutant & reference	Sensitive taxa	Responsive attribute	Measurement method	Sampling
Sulfur dioxide (LeBlanc and Rao 1975, Hale 1982, Wenmore 1983)	Lichens (e.g., <i>Xanthoparmelia cumberlandia</i>)	Disappearance of taxa Frequency of occurrence Sulfur content	Former and present range Present range and frequency Tissue analysis	From published lists and maps, from herbarium searches, and broad areawide surveys, distribution mapping Lichens to be collected from relocatable plots
Ozone (Heath 1975, Stolte and Bennett 1986)	<i>Pinus contorta</i> (lodgepole pine)	Foliage Representative leaf length % leaf retention	% leaf flecking Representative leaf length % leaf retention	Plots located within the species range using vegetation map. They should be accessible to trails or roads, have more than 30 trees which are healthy and large enough to allow repeated sampling. 5 branches are sampled from each tree.

an appropriate method of assessment of pollutant effect. The fifth column of table 15 lists such methods. Handbooks with acceptable methods must be found or developed and refined as necessary. These methods and sources are discussed later in this section.

Changes in Non-Plant AQRVs

This information is included in the decision tree to illustrate a complete permitting process. Procedures are outlined in other sections of these protocols to measure non-floristic AQRV's.

The Decision Process

With the assembled data and information sets on hand, the measurement methods can be selected. The flow diagram (fig. 9) illustrates this process with numbered steps. At step 1, the potential study species are identified by comparing the list of the flora (A) with the list of sensitive species given in the sensitivity tables (B). At step 2, the potential pollutants--those which may increase to unacceptable levels--can be derived from the air quality information (D), and at step 3, a match of this information with a list of species with known sensitivity to the appropriate pollutant (C) helps to set priorities for studies in the area of concern and leads to the identification of sites at which measurement could be made.

Sites where the sensitive species are present may be determined from the land cover and species distribution maps (B). Site selection should also consider predicted or known pollution patterns (D). If pollutant distribution data are not available, then the sensitive species must be monitored over its entire range. If the areas over which elevated pollutant levels are expected to occur overlap with the distribution of sensitive species, these areas should be intensively monitored. Those areas which are less likely to be impacted should also be

monitored. Final placement of study plots or location of samples will depend on which plant attributes are to be monitored.

Step 4 decides which measurement are to be made. Table 15 provides an example of data for set E, and lists--for two pollutants and some sensitive taxa--those attributes which are responsive or readily affected by the pollutant. For example, needle length and needle retention in *Pinus contorta* are affected by ozone levels. Similarly, step 5 decides the methods of appropriate measurement. For example, for *Pinus* foliage, the method of Stolte and Bennett (1986) using large-scale random sampling would be a good candidate.

Step 6 involves final selection of methods and measurements from among a candidate list derived in steps 4 and 5. Final selection will depend on many considerations: for example, the presence of sensitive species and attributes, the availability of effective methods, available labor and time, and coordination with other ongoing monitoring programs. Often the permit decision must be made in a very short time frame: less than a growing season. In such a case, the FLM would need to proceed to step 7.

An important decision included in step 8 is whether only short-term studies are mandated or whether long-term monitoring can be attempted. (Strategies for long-term monitoring sites are discussed later in this section.) From scientific and protection points of view, long-term studies (step 8) are desirable. They will provide the most reliable assessment of effects and also easier decisions in the case of future new permit applications and permit reviews. Therefore, it is recommended that, within constraints of funds and time, step 8 be given serious consideration. This step can be done concurrently with short-term assessments, or to build on short-term data sets gathered during expediently made permit assessments.

Following the surveys and analyses (steps 7 and/or 8) the FLM must review the information and determine, as per step 9, the health and risk of the plant components of the class I area. Other evidence (G) will be brought to bear on this by the FLM during the PSD permitting decision proper.

General Guidelines for Sampling and Analysis

Sampling and analysis will depend on the species and attributes selected in the search for sensitive systems, and also upon whether long-term monitoring or only short-term survey studies are being conducted. Within reason, we recommend that both monitoring and survey methods be as similar as possible--similar with regard to sample size and permanent marking or accurate location of sampling points or plots. Sample size should always be adequate. Methods manuals should provide information on sample size, but if new methods are developed, a competent statistician should be consulted.

Sampling along gradients of airflow, and thus along possible gradients of pollution, provides better, although never incontrovertible, evidence for cause and effect. If long-term sampling is

initiated, the pollutant can be regarded as an independent variable, and the effects of other factors such as naturally fluctuating climatic factors can be taken into account. Further information on cause and effect develops as the database grows over time, and when reliable co-measurements of physical and chemical factors are collected. The re-sampling of permanent plots and tagged individual plants over time reduces the problem of spatial variability. Most growth and physiological activities decline in late summer and early fall; sampling at this time will be the sum total of the current season's growth and can reduce some of the seasonal and temporal variability.

In most cases, potential gradients of air flow or pollution will not be known or pronounced enough to suggest where to locate sample points. Therefore, we generally favor the random placement of plots or transects within the system which contains the species of concern. Permanent marking is to be preferred and, if necessary, stubbornly lobbied for in those Class I areas where managers may object. There are markerless methods but they are costly and not always reliable. Methods of marking with minimum impact are discussed in Zedaker and Nicholas (1986). We recommend that each study plot be thoroughly described by the methods of Walker et al. (1979). These descriptions form a necessary database and give clues as to factors controlling plant stress other than pollutants. Photography of plots and individual plants is a valuable supplement to plot description. Photographs can record for posterity what the observer has not yet learned to spot, or what does not seem important at the time.

Table 15 illustrates the types and methods of measurement which could be used for the two pollutants--ozone and sulfur dioxide. The table further illustrates the kinds of considerations that FLMs and experts will need to make in deciding an appropriate measurement and its sampling method. The annotations concerning ozone and sulfur dioxide effects help illustrate the process of method selection.

Ozone does not leave a residue within the plant to be measured, whereas sulfur dioxide may be retained as sulfate or some other sulfur compound. Therefore, tissue chemistry is not useful for ozone detection; assays of products of oxidation from ozone injury are not appropriate in field techniques since the products are ephemeral. Lichens and bryophytes have not been shown to be sensitive to ozone and would not, therefore, not be used in an assessment of ozone effects. Some pines, however, are sensitive to both sulfur dioxide and ozone, and assessment methods could be combined (see Stolte and Bennett 1986). We recommend the Milkweed measurement method of Bennett and Stolte (1985) as a model of an assessment method.

Analysis of tree rings for accumulated trace metals (Berish and Ragsdale 1985) and analysis for reduced growth resulting from poor air quality (Nash et al. 1975) are attractive methods since they have the potential to show previous regimes of effects of pollutants on growth. Generally, however, we caution against tree ring

analysis since it is technically demanding and expensive. Also, cross-contamination of tree rings is possible and any reduced growth effects can seldom be related to specific pollutants.

Perhaps the most difficult part of the plant protocols will be the determination of the significance of observed plant responses, and what the continued or ultimate consequences or those responses imply for the plant population. It is upon these prognoses that the permitting decision will rest.

Long-Term Monitoring: Measures and Basic Sampling Design

When a specific pollutant is not identified, or for such concerns as acid deposition that may cause ecosystem-level effects, it is recommended that a basic and long-term monitoring effort be conducted.

The original list of the flora (data set A) should be field checked. Special care should be taken to have correct identification and herbarium archiving to avoid incorrect conclusions about future losses of species.

Table 16 lists the principal attributes recommended for measurement. Tables 17 and 18 and figures 10, 11, and 12 provide some sample forms and scales for plot description by the releve method (Walker et al. 1979). A releve is

Table 16.--Measurements for vegetation and plant monitoring.

Attribute	Method	Reference
<u>Vegetation Map Units</u>		
Species composition	Releve	Walker et al. 1979
Site factors	Releve	Walker et al. 1979
Soils and geology	See Work Group 2	
<u>Permanent Plots (50X50m)</u>		
Photographs		Walker et al. 1979
Site factors		Walker et al. 1979
Soil	See Work Group 2	
Species Composition		Walker et al. 1979
- Cover value for shrubs, herbs, and ground layer		
- Density and diameters for trees		
<u>Fruticose and Foliose Lichen Plots (20X25 cm)</u>		
Photographs	35 mm camera	Hale 1982
Species check list	Listing	Hale 1982
Plant Chemistry		
- Pb, Cd, Zn, Ni, Cu, Mn	Atomic absorption	Allen et al. 1986
- Sulfur	ashing and HNO ₃ Leco combustion to SO ₂	See Work Group 2
<u>Evergreen Plants</u>		
Leaf necroses and chloroses	Comparison with color standards	e.g., Jacobson and Hill 1970
Elemental analysis	Atomic absorption	Allen et al. 1986
Leaf retention by age class	ashing and HNO ₃ See text	
<u>Trees</u>		
Tree ring growth analysis for each site	Tree coring and dendroecology	Nash et al. 1975
Historical record of pollutant deposition Pb, Cd, Zn, Ni, Cu, Mn,	Ashing and HNO ₃ , atomic absorption	Berish et al. 1985

Table 17.--Subjective environmental gradient scales to be used for completion of figure 10.

Site scale	Site moisture	Soil moisture	Summer Air temperature	Snow	Wind
1	Very dry, little or no moisture within 10 cm of surface, exposed to strong winds	Very dry, no apparent moisture, no clumping	Very cold sites, high altitude with north-facing slopes	Little or no snow cover in winter, ridge top sites	Completely sheltered from the wind
2	Very dry, little moisture near surface, somewhat less exposed sites	Very dry, some moisture but doesn't clump	Cold sites, high altitude with moderate solar exposure, north-facing coastal plain sites or flat sites extreme arctic coast	Little or no snow cover in winter, exposed slopes	Exposed to occasional very light (1-5km/hr) winds
3	Dry, some moisture near the surface, very exposed	Dry, clumps but then crumbles	Cold sites, moderate altitude flat coastal plain sites	Slopes usually snow covered in winter	Very light winds common
4	Dry, some moisture near the surface, somewhat less exposed sites	Dry, clumps and stays in a ball	Cool sites, flat surface in Arctic Foothills	Slopes snow covered in winter, snow melt by late May	Occasional light (5-10 km/hr) winds
5	Moist, top 10 cm continually moist to wet, moderately well-drained sites	Moist, binds but can be taken apart	Moderate temperatures, south-facing slopes on Arctic Coastal Plain or high mountains	Shallow depressions, somewhat prolonged snow cover, melt by early June	Light winds common
6	Moist, top 10 cm near saturation, less well-drained sites	Moist, binds completely into goeey ball	Moderate temperatures, south-facing slope, Arctic Foothills	Snow patches, snow melt by late June or early July	Occasional moderate (20-30km/hr) winds
7	Wet, continually saturated soil but no standing water	Wet, can squeeze some water out	Moderate temperatures, flat site at intermediate altitudes south of Brooks Range	Snow patches somewhat later snow melt by late July	Moderate winds common
8	Wet, usually with standing water early in summer	Wet, can squeeze lots of water out	Warm temperatures, flat site, lower altitudes south of Brooks Range	Snow patches, later snow melt, early August	Occasional strong winds (40-50km/hr), winds otherwise light
9	Very wet, usually with standing water late in summer	Very wet, totally saturated	Warm, south-facing slopes at intermediate altitudes in interior Alaska	Snow patches, very late snow melt, late August	Strong winds common, winds otherwise moderate
10	Very wet, deep standing water year round	Very wet, soil taken from under-water	Warmest south-facing slopes at lower altitudes in interior Alaska	Snow patches, very late snow melt, sometimes may have snow cover all year	Strong winds common, occasional very strong (>60km/hr) winds

Table 17.—Continued.

Site scale	Surface age	Stability	Cryoturbation	Fire	Overall vegetation	Tree layer	Shrub layer	Herb layer	Ground layer
1	Constant disturbance	Completely unstable always moving (e.g., dunes)	0% of surface disturbed	No evidence	Barren, very sparse vegetation	Scattered small trees (<5cm dbh)	Shrubs rare	Very widely scattered herbs	Very sparse
2	Less than 1 yr. since severe disturbance	Annually unstable (e.g., avalanche slopes, river bars)	< 1%	Buried charcoal	Prostrate scrub or lichen meadow	Scattered medium trees (5–15cm dbh)	Scattered dwarf shrubs (0.1–0.5m)	Scattered short herbs (<0.1m)	Scattered
3	1 – 10 yrs	Periodically unstable (e.g., 50-yr flood plain)	1–2%	Charcoal on surface rare	Graminoid meadow	Open small trees	Scattered medium shrubs (0.5–2m)	Open short herbs	Open thin cover (<2cm)
4	10 to 100 yrs	Unstable, vegetation in patches, on slope	2–5%	Charcoal on surface common	Tussock graminoid meadow with thick moss	Closed small trees	Open dwarf shrubs	Closed short herbs	Closed thin cover
5	100 to 1000 yrs, last disturbance during late Holocene	Unstable, vegetation in patches, on flat	5–10%	Older burn, living trees have burn scars	Dwarf scrub	Scattered large trees (>15cm dbh)	Closed dwarf shrubs	Open medium herbs (0.1–5m)	Open moderate thickness (2–5cm)
6	1000 to 10,000 yrs, last disturbance during early to mid-Holocene	Moderately stable, open vegetation, on slope	10–15%	Older burn, regrowth of large trees (>15cm dbh)	Scrub	Open medium trees	Scattered tall shrubs (>2m)	Closed medium herbs ate thickness	Closed moder-
7	Old surface, last disturbance during late Wisconsin (30,000 yrs B.P.)	Moderately stable, open vegetation, on flat	15–25%	Older burn, regrowth of moderate-sized trees (5–15cm dbh)	Dense tall scrub or open small evergreen trees	Closed medium trees	Open medium shrubs	Open tall herbs (0.5–1m)	Open thick (5–15cm)
8	Old surface, last disturbance during early Wisconsin (30,000 – 70,000 yrs B.P.)	Stable surface, completely vegetated, moderate slope	25–50%	Recent burn, small trees and/or complete vegetation cover	Open medium-sized trees or dense small tree (<5cm dbh)	Open large trees (>15cm dbh)	Closed medium shrubs	Closed tall herbs (0.5–1m)	Closed thick
9	Very old surface, last disturbance during pre-Wisconsin time	Stable surface, completely vegetated, slight slope	50–75%	Recent burn, no regrowth of trees	Open large trees (>15cm dbh) or dense medium-sized trees (5–15cm dbh)	Closed large trees	Open tall shrubs	Open very tall herbs (>1m)	Open very thick (>15cm)
10	Very old unglaciated surface	Most stable surfaces, completely vegetated, flat	75–100%	Complete burn, no regrowth	Dense large trees (>15cm dbh)	Closed very large trees (>25cm dbh)	Closed tall shrubs	Closed very tall herbs	Closed very thick

Animal scales: 0 No sign

1 Slight evidence

2 Moderate evidence

3 Abundant evidence

Figure 10.--Sample form for releve site factors.

Releve No. _____ Map Name _____

Observer _____ Date _____

Master Map Code _____ Map Unit No. _____

Site Description and Site Factor Code (see Table 4-7) _____

Sample Area _____ Depth of Thaw _____

Slope Aspect _____ inclination^o _____ Depth of Water _____

Site Scale (1-10):
(see Table 4-4)

Relief:
site moisture _____ Microrelief:
soil moisture _____ Type _____
temperature _____ Height _____ Width _____
snow _____ Mesorelief:
wind _____ Type _____
surface age _____ Height _____ Width _____
stability _____
cryoturbation _____
fire _____ (fire evidence _____)

Vegetation:
Age of Vegetation: Estimate _____ Evidence _____

Percentage Cover: Height:
All vegetation _____ Tree layer(m) _____
Trees(>2m) _____ Shrub layer(m) _____
Tall shrubs(>2m) _____ Herb layer(cm) _____
Medium shrubs(.5-2m) _____ Ground layer(cm) _____
Dwarf shrubs(10-15cm) _____

Prostrate shrubs(<10cm) _____ Biomass (scale 1-10):
Graminoids _____ Overall _____
Forbs _____ Tree layer _____
Bryophytes _____ Shrub layer _____
Lichens _____ Herb layer _____
Rocks _____ Ground layer _____
Bare soil _____
Water _____ Photo Nos. _____

Table 18.--General landforms.

20 Dunes	55 Valley
21 active	56 depositional
22 inactive	57 erosional
25 Basin/depression	60 Mesa
26 thermokarst basin	61 footslope
30 Plains	62 sideslope
31 depositional	63 crest
32 erosional	70 Hills
35 Flood plain	71 footslope
36 channel	72 sideslope
37 active	73 crest
38 abandoned	80 Mountain
39 river bar/island	81 footslope
40 River terrace	82 sideslope
41 depositional	83 crest
42 erosional	98 Water
45 small delta	
50 Alluvial fan	
51 active	
52 inactive	

literally a "picture" of a plot or stand. These tables and scales were designed for an Alaskan research program, and serve only as a starting point for the FLM and must be modified for each new area. The basic sampling design calls for

Figure 10.--Continued

Releve No. _____

Animals:

Name	Scale (0-3)	Evidence
Bear	_____	_____
Caribou	_____	_____
Moose	_____	_____
Lemmings	_____	_____
Microtines	_____	_____
Ground squirrels	_____	_____
Ptarmigan	_____	_____
Other birds	_____	_____
Insects	_____	_____
Others	_____	_____

Plant Phenology:

Species	Stage
_____	_____
_____	_____
_____	_____
_____	_____

Soil:

Soil type _____ Parent material _____

Description (include horizon names, depths, color, texture, structure, character of boundaries, %rocks, %fiber, %mottles):

Photo Nos. _____ Soil sample top 10 cm _____

Disturbance:

Type	Age
_____	_____

Notes _____

Checklist:

() Mark location on photo	() Soil photo
() Mark location on map	() Vascular plant sample
() Soil sample	() Moss sample
() Tree core	() Lichen sample
() Vegetation photo	() Permanent plot staked & marked

several equivalent landscape units, such as small alpine basins, to be surveyed and mapped. These units should be selected, wherever possible, along known or predicted airflow paths where gradients of pollution might be expected. Permanent plots that contain the growth forms being studied should be established within each basin. These growth forms are fruticose and foliose lichens, evergreen plants, and trees. Individual plants or plant parts must be permanently tagged or able to be reliably re-identified.

Requirements

Estimates of person-day and field equipment requirements are given in tables 19 and 20. These estimates may be rather low, and may need to be increased for sites with poor accessibility.

Field Methods

The initial regional survey of plot establishment should be done during the first growing season. Plots should be accessible but

Releve/Plot Number _____

[illegible]

Table 19.—Manpower estimates for long-term studies in a wilderness area with average access.

Personnel	Number of person-days/year	
	Year 1	Years 2-10
Plant Ecologist	50	5
Plant Taxonomist	15	5
Field Assistant	50	20
Chemistry Technician	30	25
Draftsman/Cartographer	10	0

Collection No. _____ Herbarium No. _____

Plant Name _____

Field Name _____

Locality _____ Releve/Plot No. _____

Longitude _____ Latitude _____ Altitude _____

Ecol. Notes: Moisture _____ Slope _____

Community _____

Collectors _____

Date _____

Landscape Unit Mapping.--Aerial survey, local interviews, and small-scale topographic maps are used to select candidate landscape units. This selection should be made in cooperation with Soils and Geology and Aquatic Chemistry and Biology. Small, well-defined valleys containing forests and meadows with surrounding uplands would provide the required sample plots. Reconnaissance visits are required to make final unit selections. Several (at least five) landscape units should be selected along known airflow paths. Additional (up to five) units could be located in a cluster at the center of the airflow path. These additional units would serve to establish spatial and other natural variation of attributes.

Table 20.—Field equipment and materials.

Mapping

Topographic maps (1:24,000), color infra-red aerial photographs (1:60,000), mylar overlays for photographs with provisional and classification boundaries, map unit releve forms, plant collection bags, plant tags, local flora, plant press, acetate pens, pencil and notebook.

Permanent Plots

Transit and stadia rods, 50 m steel tapes, PVC pipe or steel re-bar stakes, metal plot tags, engraving tool, 35 mm camera, color film, diameter tape, releve forms, plant collection bags, plant tags, plant press, pencil and notebook.

Lichen Plots

Hammer and star-rock drill, 20X25 cm quadrat frame, 35 mm camera, color film, stainless steel plot tags, engraving tool, collecting bags, species check list forms.

Evergreen Plants

Notebook and pencil, stainless steel plant tags, engraving tool, plant pathology comparison charts, 30 cm rule graduated in mm, notebook and pencil, collecting bags.

Trees

Teflon-coated increment corer (16"), solvent and distilled water in squirt bottle, plastic drinking straws, carrying case for wood cores, metal tree tags, engraving tool, 35 mm camera, film, pencil and notebook.

Following field checking and appropriate updating, boundaries can be easily transferred to a 1:24,000 USGS topographic base map.

Each final map unit should be characterized for vegetation and landform cover. The method of Walker et al. (1979), which uses the releve technique (Westhoff and Maarel 1978), is quick and appropriate (tables 17 and 18, figs. 11 and 12).

Voucher collections should be made when rare plants or plants of uncertain identity are encountered. Standard herbarium techniques should be used. Figure 11 gives the needed plant collection information.

Soil information can be readily added to these geobotanical maps.

Mapping of each basin will require about 0.25 man days of aerial photo interpretation and 4 person days of field effort. Final plant determinations and drafting should be done in the laboratory.

Large plot location and description. In each landscape unit, large 50 X 50 m permanent plots should be located and established. These should contain good stands of fruticose and foliose lichens, evergreen plants (both shrubs and trees), and mature forest trees. In each unit a minimum of five plots should be set up to provide access to the required taxa. All taxa might be contained in a single plot. Plots should be staked, tagged, located precisely on the geobotanical maps, and reference sightings made to prominent terrain features. A series of oblique photographs should record general aspect and vegetation of each plot. Each plot should be described with the releve method, which will provide a complete inventory of flora and estimates of individual species abundance. Cover values should be recorded for shrubs, herbs, and ground layers. Trees should be recorded by species, number, and dbh (diameter at breast height).

Set-up and description of each plot should take about 0.25 person-day.

Attribute Sampling and Monitoring

Lichens. Ten small 20 X 25 cm microplots should be set up in each of the five larger (50 X 50 m) macro-plots to record ground and rock lichen communities. The plots can be marked with small stainless steel stakes or small holes in rock surfaces using a star-rock drill and hammer. The basic method is that of Hale (1982). Vertical whole plot photographs and oblique aspect photographs should be taken for each plot. A complete as possible listing of lichens is made. Voucher collections should be made outside of the microplots. A large handful (5-10 g) of each common fruticose or foliose lichen is collected from within each 50 X 50 m plot for elemental analysis (see table 16). Samples should not be collected into brown kraft paper bags because of the possibility of sulfur contamination. Similarly, zinc contamination may result from using ordinary plastic bags. Synthetic bags made of materials such as tyvek are preferable. The bags should "breathe" and the lichens should be dried in the bag. Foreign

material (other lichens, insect cases, moss, etc.) should not be removed from air-dried specimens. Specimens should not be oven-dried or washed. Samples should be ground in a Wiley mill to pass a 20-mesh screen.

Setting up and recording 10 microplots in each macroplot and sampling for elemental content of lichens takes about 0.5 of a man day.

Evergreen foliage. Evergreen species should be sampled within the macroplots available. Evergreen shrubs or trees are best; evergreen herbs are of dubious value. When possible, the same species should be used throughout a wilderness area. Ten individual plants should be tagged and their locations recorded in a macroplot. Ten individual branches should also be tagged on each plant to allow for replication and future repeated measurements. Photographs of each individual plant should be taken.

Each branch is examined against standard color charts and photographs of leaf damage from known pollution effects, and scored for signs of necrosis (flecking, tip-die-back, etc.) and chlorosis. Further literature and method development is needed here. A good start is Miller and McBride (1975).

Samples of leaves of each age class (about 20 grams fresh weight) should be taken from neighboring unmarked plants. Dead and living leaves should be collected separately. Five samples per macroplot are recommended.

A record should be made of leaf numbers per age class for each marked branch.

Tree wood. Methods of tree coring and wood trace element analysis are well worked out by Berisch and Ragsdale (1985). Within the 5 macroplots, 10 trees of each dominant species should each be cored 3 times at breast height. Two of the three cores are used for element analysis in 5-year increments, and the remaining core is used for growth analysis. In subsequent years, only short cores will be necessary. Each tree should be photographed, tagged, and its location recorded. Coring of 20 trees takes about 0.5 man day.

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Rocky
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Southwest



Great
Plains

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Rocky Mountain Forest and Range Experiment Station

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Herded vs. Unherded Sheep Grazing Systems on an Alpine Range in Wyoming

John F. Thilenius and Gary R. Brown



Herded vs. Unherded Sheep Grazing Systems on an Alpine Range in Wyoming

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Rocky Mountain Forest and Range Experiment Station

Abstract

The influence of sheep grazing on plant composition, canopy coverage, and forage utilization, was studied on an alpine range in northwestern Wyoming grazed by an unherded band of sheep and on an adjacent range where the sheep were grazed under the usual herded system. Under both systems total canopy coverage did not change appreciably over the 10 years of study. Alpine mat clovers, graminoids, and grasses were the preferred forages. Overall forage utilization was low; 6.1% on the range where the sheep were herded and 8.1% on the range grazed by the unherded sheep. Protecting range from sheep grazing influenced plant composition, but not total canopy coverage. The major response to protection from grazing was a decline in the coverage of alpine mat clovers, accompanied by an increase in the coverage of other forbs, especially non-cushion plant forbs. Lamb weight gains were similar under both grazing systems.

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INTRODUCTION

Sheep are the principal domestic grazing animal in the alpine zone of western North America (Thilenius 1975a). Historically and currently most sheep are grazed under the control of a herder. Thus, whether or not proper range management is applied depends to a great extent upon the experience and desire of the herder and upon the control exercised by the livestock owner and by the land management agency that administers the range.

Because qualified, responsible herders may be difficult to employ, herderless grazing has been advocated (Jones and Paddock 1966). Under this system the sheep are turned loose onto the range and allowed to distribute themselves and graze according to their own wants. Herderless grazing is not new. Jardine (1912) reported on a 5-year study on high mountain ranges in eastern Oregon, and the practice is normal in the mountains of New Zealand and Scotland. Advantages claimed for herderless grazing are better distribution of sheep over the range; minimal concentration on bedgrounds; decreased trailing damage; and better weight gains on lambs. Disadvantages are the need for fencing or natural barriers to limit unwanted movement (on alpine ranges, especially, fences may be expensive and difficult to build and maintain); increased possibility of predation; difficulty in collecting the sheep at the end of the grazing season; potential for grazing or bedding on areas that should be considered as nonrange, such as steep, easily eroded slopes, wet boggy areas below snowbanks, or riparian sites (Thilenius 1975a).

With these factors in mind, this study was initiated to determine if sheep could be successfully grazed on alpine ranges in northwest Wyoming without the continuous attention of a herder. Considered in the study were the influence of sheep grazing on range plant composition, canopy crown coverage, forage utilization, and lamb weight gains. These were recorded on an alpine range grazed by an unherded band of sheep and on an adjacent alpine range where sheep were grazed under a normal herded system. As an adjunct study, permanent sheep exclosures were established on each range to show how exclusion from sheep grazing influenced the vegetation.

STUDY AREA

The study was conducted on the eastern edge of the Absaroka Range at the eastern extreme of a long (ca. 32 km) northeast-southwest trending ridge of volcanic material known as Carter Mountain. The terrain of the study area is almost level to moderately steep. Slopes greater than 30% do occur, but none is inaccessible to sheep. Maximum elevation is 3445 m, but most of the range is below 3350 m. The total area of both allotments is approximately 1640 ha.

True alpine vegetation begins at 3050 m elevation. For the most part the alpine vegetation belongs to the turf and cushion plant physiognomic types. The plant communities, which are primarily examples of dry site alpine vegetation, and the soils have been described by Thilenius and Smith (1985).

Part of the dry condition of the range is due to its exposure to the prevailing westerly winds of winter, which leave much of the area snow-free. Compounding this is the fragmented nature of the volcanic substratum, which promotes good to excessive substrate drainage conditions throughout the range. The study site has no permanent bodies of water and only one mesic meadow about 10 ha in area. Small watercourses run full during the snowmelt period of May to mid-June, but during July and August there is little water in drainages except immediately after rainstorms. Even areas immediately below many of the long-lying snowbanks are not excessively moist throughout most of the summer. There are, however, several large permanent springs in the area. These originate in a band of volcanic ash exposed at the 3100-m level. Three water developments were built on this exposed aquifer to aid in the distribution of the unherded sheep band.

The entire range, which had been a Shoshone National Forest sheep allotment for many years under a herded management system, was subdivided for this study into two grazing allotments. The more eastern, referred to as the Carter Mountain allotment, was assigned to the unherded sheep band; the allotment used by the herded band was called the Meeteetse Creek allotment. Fences were constructed between the allotments to keep the unherded sheep out of Meeteetse Creek allotment and

on the Carter Mountain allotment to block the movement of the unherded sheep to the north. The western boundary of the Meeteetse Creek allotment was unfenced, but was marked by rock cairns to indicate to the herder the limits of the assigned grazing area.

METHODS

Grazing Systems

Sheep grazed the allotments between July 10 and September 8 (60 days). This is the normal grazing period for alpine grazing allotments on the Shoshone National Forest. The average length of time the sheep actually were in the alpine zone was closer to 50 days as they usually were moved to lower ranges soon after September 1. The sheep bands averaged 1200 ewes plus their lambs. As twin lambs were common, there were about 3000 animals in each band. The herded band was moved by the herder from a base camp at 2400 m to the alpine zone (+3050 m) in a single day. The unherded sheep were released at the 2400-m level, and normally reached the study area in a day. Unherded sheep remained at the highest elevations on the allotment for most of the grazing period.

Vegetation Sampling

Measurements of vegetation on the open range were made at 149 sites: 75 on the Meeteetse Creek allotment; 74 on the Carter Mountain allotment (one site was destroyed by a bulldozer during road construction for seismic oil exploration). Estimations were made in 1965, 1970, and 1975 in mid-July when the majority of the taxa were best developed.

At each site, canopy coverage was estimated on ten, 1x2-dm quadrats systematically located at 3-m intervals along a 30-m transect line. Estimation intervals were 10% for canopy coverage greater than 10%. Intervals of less than 1% and between 1% and 10% were used to estimate coverage below 10%. Estimations were made on the basis of plant groups. The plant groups were (1) geum, which consisted of only *Geum rossii*, the most obvious single taxon; (2) mat clovers (*Trifolium* spp.), which were the most heavily grazed taxa according to Strasia et al. (1970); (3) cushion forbs; (4) non-cushion forbs; (5) true grasses; and (6) graminoids (sedges, rush, and woodrush). The individual taxa included in each plant group are given in the Appendix. Specimens of all taxa encountered were collected and deposited in the herbarium of the Forest Range and Watershed Laboratory, Laramie, Wyo. Identifications were checked by the Forest Service Herbarium, Washington, D.C., and Fort Collins, Colo.

Utilization was estimated on the same 149 sites used to estimate canopy coverage, but twenty 4x8-dm quadrats were used. The utilization quadrats were spaced 1.5 m apart along a 60-m transect partly superimposed on the coverage estimation transects. A record was made of all of the taxa present on the quadrats whether utilized or

not, but the amount of foliage removed was estimated only for the plant groups. Utilization was estimated in September as soon as possible after the sheep had left the range.

A more intensive study of the vegetation was conducted at a 30x30-m sheep enclosure in each allotment. Quadrat size and canopy coverage estimation techniques were the same as for the open range, but the number of quadrats was increased from 10 to 20 each, inside and outside the enclosures. The initial measurements of coverage inside the enclosures represent vegetation protected from grazing by sheep for one growing season.

The "outside enclosure" study sites were grazed by sheep. It is possible the presence of an artificial barrier in very open terrain attracted the unherded sheep, but we have assumed the intensity of use outside the enclosure was not biased by the presence of the fence.

Analysis of variance was used to test the statistical significance of differences in canopy coverage and utilization for the six plant groups. The 0.05 level was used to determine statistical significance.

Animal Performance

As an additional evaluation of the two grazing systems, the weight gain of a randomly selected sample of 100 lambs from each herd was determined. The lambs were ear-tagged and weighed to the nearest 0.45 kg (1 lb) at the beginning and end of the grazing season. Because the length of the season varied from year to year, gains were calculated as a daily average. Analysis of covariance was used to compensate for difference in initial weight. Statistical significance was 0.05.

RESULTS

Composition and Canopy Coverage

The taxa composition, physiognomy, and distribution of plants was sufficiently different between the two allotments to give the vegetation a generally different overall appearance. On the Meeteetse Creek allotment, the vegetation was somewhat taller and more lush than on the Carter Mountain allotment. The Meeteetse Creek allotment had a greater area of shaded lee slopes where long-lasting snowbanks were present. Consequently, a better supply of available water was present during the growing season. The Carter Mountain allotment was located at the end of an exposed, windswept ridge and large long-lasting snowbanks were uncommon.

Major Plant Taxa

Ninety-four taxa were recorded on 149 sampling sites (Appendix), but only eight taxa had an overall average canopy coverage that exceeded 2%. *Geum rossii* (11.4%), *Trifolium dasyphyllum* (9.8%), *T. nanum* (8.1%), *Poa* spp. (5.5%), *Carex obtusata* (3.5%), *Polygonum bistortoides*

(3.0%), *Arenaria obtusiloba* (2.6%), *Lomatium montanum* (2.1%). All are common in alpine tundra of northeastern Wyoming. The eight taxa provided 63% of the total canopy coverage of the combined allotments. The first three listed provided 40% of canopy coverage. Concentration of total plant abundance in a few taxa is common in alpine vegetation (Thilenius and Smith 1985).

The canopy coverage of *Poa* spp. is somewhat misleading. Three species (*P. alpina*, *P. rupicola*, and *P. cusickii*) were combined into one taxon because of general absence of flowers and consequent uncertain identification. *Koeleria cristata* (1.7%) had the greatest canopy coverage of all individual grass species. The grass *Deschampsia caespitosa*, which is considered to be a key species for the evaluation of condition and trend on alpine ranges in the Rocky Mountains (Schwan and Costello 1951), was rare on both allotments.

Plant Groups

In 1965, geum, non-cushion forbs, and graminoids had significantly higher canopy coverage on the Meeteetse Creek allotment, while cushion forbs had significantly greater canopy coverage on the Carter Mountain allotment (table 1). There were no differences in the canopy coverage of alpine mat clovers and grasses.

Canopy coverage of geum, grasses, and graminoids was statistically similar on the two allotments in 1970. The Meeteetse Creek allotment had a significantly greater canopy coverage only of non-cushion forbs. Alpine mat clovers and cushion forbs had significantly greater canopy coverage on the Carter Mountain allotment.

In 1975, the canopy of geum, non-cushion forbs, grasses, and graminoids was significantly greater on the Meeteetse Creek allotment. The Carter Mountain allotment had significantly greater canopy coverage of alpine mat clovers and cushion forbs.

Overall, the Meeteetse Creek allotment had the greater canopy coverage of geum, non-cushion forbs, and graminoids; the Carter Mountain allotment had significantly more alpine mat clovers and cushion forbs. Canopy coverage of grasses was the same on both allotments.

On the Meeteetse Creek allotment there were no statistically significant differences in the canopy coverage of the geum, alpine mat clover, cushion forb, and graminoids plant groups between the three sample periods. Grasses had a statistically significant higher canopy coverage at the middle sample period, but there was no statistically significant difference in grass canopy coverage between the first and last sample periods. The canopy coverage of non-cushion forbs did not change

Table 1.—Average percentage canopy coverage and standard deviation as estimated by plant groups on the Meeteetse Creek (herded) and Carter Mountain (unherded) allotments, 1965–1975.¹

Year	Plant group	Meeteetse Creek		Carter Mountain	
		x	s	x	s
1965	Geum	12.5*	9.9	8.6	6.5
	Non-cushion forbs	20.6*	9.9	17.3	8.1
	Mat clovers	19.1	11.8	21.4	11.5
	Cushion forbs	6.1	4.7	8.2*	4.3
	Grasses	9.1	5.5	8.0	4.4
	Graminoids	7.9*	5.6	4.9	3.3
	All groups	75.3		68.4	
1970	Geum	12.9	9.9	10.7	7.6
	Non-cushion forbs	23.5*	13.3	9.0	7.5
	Mat clovers	17.7	11.5	23.3*	14.7
	Cushion forbs	6.7	5.2	11.8*	10.0
	Grasses	11.4	5.8	10.8	6.0
	Graminoids	9.0	7.1	7.5	5.8
	All groups	81.2		73.1	
1975	Geum	13.5*	9.9	10.3	7.1
	Non-cushion forbs	16.8*	11.1	10.0	7.7
	Mat clovers	15.5	10.9	20.6	13.6
	Cushion forbs	6.7	5.1	11.4*	5.9
	Grasses	8.3*	5.0	6.7	3.4
	Graminoids	7.3	4.7	4.3	3.1
	All groups	68.1		63.3	

*Statistically higher canopy coverage between allotments.

¹Before study was started in 1965 both ranges had been grazed under a herded system for many years.

significantly between the first and second sample periods, but it was significantly greater at the last sample period.

On the Carter Mountain allotment there were no significant changes in the canopy coverage of geum and alpine mat clovers. Non-cushion forbs and cushion forbs had significantly higher canopy coverage at the beginning of the study period than at both of the two later sample periods. Differences in canopy coverage of non-cushion forbs and cushion forbs between the two later periods were nonsignificant. Graminoid canopy coverage was significantly greater at the middle sample period, but no significant difference was present between the first and last sample periods. The canopy coverage of grasses also was significantly greater at the middle sample period than at the first and last periods and there was significantly greater canopy coverage of grasses at the initial sample period than there was at the last sample period.

Effects of Grazing

Forage Utilization

The estimates of forage utilization were made in mid-September after the sheep had left the range. Early fall snowstorms prevented estimation of utilization in 1968, 1970, 1971, and 1973.

Overall, mat clovers were the most utilized plant group, graminoids second, and grasses third (table 2). Non-cushion forbs and geum were ranked next. Utilization of geum was significantly greater on the Carter Mountain allotment. It was the only group to show a statistically significant difference in utilization between allotments. Very little use was recorded on cushion forbs, possibly for reasons similar to those given for non-cushion forbs and partly because their woody stems and prostrate growth form makes them unpalatable or ungrazable.

Responses of Plant Groups

The responses of the six plant groups to protection from sheep grazing are shown in table 3. In general, the

geum and non-cushion forb plant groups significantly increased canopy coverage when sheep grazing was eliminated. This was particularly true at the Meeteetse Creek enclosure, where these two plant groups were most abundant. Both significantly increased in canopy coverage on the grazed area at the Meeteetse Creek enclosure and on the protected area at the Carter Mountain enclosure.

The canopy coverage of the geum and non-cushion forb plant groups outside the Carter Mountain enclosure was so low it was impossible to determine any effect of grazing. The differences in canopy coverage of both plant groups between the inside and outside of the Carter Mountain enclosure were attributed to growing conditions, not grazing.

When not grazed, canopy coverage of the mat clover plant groups significantly decreased at the Meeteetse Creek enclosure. In the ungrazed site at the Carter Mountain enclosure mat clover canopy coverage was maintained. Mat clovers generally maintained canopy coverage under grazing. Although there was a statistically significant increase in canopy coverage of alpine mat clovers with grazing at the Meeteetse Creek enclosure and a significant decrease at the Carter Mountain enclosure, the absolute changes in canopy coverage were small.

At both enclosure sites the canopy coverage of cushion forbs fluctuated more and decreased when protected from sheep grazing. In the grazed sites, canopy coverage of cushion forbs was maintained at much the same levels. A very small, but statistically significant increase in canopy coverage of cushion forbs occurred on the grazed site at the Meeteetse Creek enclosure.

Although some statistically significant changes in the canopy coverage of grasses and graminoids did occur at both enclosure sites, there were no strong trends or large differences in canopy coverage on either grazed or ungrazed sites.

Lamb Weight Gains

The overall average weight gains of lambs were the same (0.14 kg/day) on both the Meeteetse Creek (herded

Table 2.—Average percentage occurrence and percentage utilization of plant groups on the Meeteetse Creek (herded) and Carter Mountain (unherded) allotments between 1965 and 1975.¹

Plant group	Meeteetse Creek		Carter Mountain	
	Percent occurrence	Percent utilization	Percent occurrence	Percent utilization
Mat clovers	90	16.4	93	19.4
Graminoids	91	8.4	94	11.0
Grasses	88	5.0	92	8.6
Non-cushion forbs	56	3.7	64	5.2
Geum	68	2.4	81	5.8
Cushion forbs	7	0.1	9	0.3

¹Utilization was estimated after sheep had left the ranges. Not estimated 1968, 1970, 1971 and 1973 because all sites were covered by snow.

Table 3.—Percent of canopy coverage of plant groups at the Meeteetse Creek and Carter Mountain exclosures, 1965, 1970, 1975.

Plant group	1965				1970				1975			
	Inside	s	Outside	s	Inside	s	Outside	s	Inside	s	Outside	s
Meeteetse Creek Allotment (herded)												
Geum	15.5	4.0	9.0	3.0	14.1	5.4	14.4	5.9	18.3	6.6	13.9	6.6
Non-cushion forbs	11.8	3.1	3.7	1.1	19.8	3.6	11.6	2.9	26.3	10.0	14.5	7.3
Mat clovers	24.9	6.2	15.1	6.0	20.6	6.0	19.0	5.4	14.8	5.5	18.9	10.1
Cushion forbs	6.3	2.1	5.5	1.6	1.3	1.3	5.3	2.2	4.3	1.7	7.5	3.2
Grasses	9.2	2.4	3.7	1.2	7.2	2.5	5.3	2.6	6.0	2.1	4.4	2.7
Graminoids	6.6	3.4	4.9	1.4	9.1	3.6	8.1	3.2	6.4	3.0	7.3	3.7
All groups	74.3	7.0	41.9	4.4	72.1	7.6	63.7	5.5	76.1	8.7	66.5	5.5
Carter Mountain Allotment (unherded)												
Geum	7.1	3.4	0.5	1.4	10.3	5.3	0.7	0.2	11.5	6.1	1.1	2.4
Non-cushion forbs	5.3	2.0	3.4	0.9	14.7	6.2	2.9	2.9	13.9	4.3	5.8	3.8
Mat clovers	15.9	6.8	18.6	5.2	14.0	7.6	13.5	3.7	12.6	5.6	15.6	8.8
Cushion forbs	11.7	4.2	13.1	5.2	4.4	2.9	12.6	3.6	7.8	3.6	17.1	9.1
Grasses	5.3	1.6	5.1	5.4	4.3	2.0	4.1	1.6	5.1	1.9	3.2	1.8
Graminoids	4.6	1.5	5.1	1.2	4.2	1.7	5.7	1.4	5.5	1.8	3.9	1.8
All groups	49.9	4.5	45.8	6.8	51.9	5.0	39.5	5.3	56.4	3.8	46.7	6.8

grazing) and Carter Mountain (unherded grazing) allotments. Lambs on the Meeteetse Creek allotment had significantly greater gains in 1965, 1970, and 1972, while lambs on the Carter Mountain allotment outgained those on Meeteetse Creek in 1967, 1974, and 1975. There were no significant differences in the remaining 5 years.

DISCUSSION

Total plant coverage on either of the two allotments did not change appreciably over the 10 years of study under either system of grazing. The slightly higher total canopy coverage on the range grazed under a herded system should be attributed to the slightly better growing conditions rather than to the grazing system. Although there is some difficulty in using measurements taken at periods widely separated in time to express trends, the patterns in total plant coverage were similar for both ranges. Changes in absolute coverage were not significantly large, and the growing conditions of the year the samples were obtained seemed to be more influential than the grazing systems.

Geum and alpine mat clovers were the most important plant group at all three sample periods on both ranges. A major compositional difference between the allotments was the greater coverage of alpine mat clovers on the Carter Mountain allotment where the sheep were unherded. The Carter Mountain allotment also had greater coverage of cushion plants. Non-cushion forbs had greater coverage on the Meeteetse Creek range.

Average utilization for all classes of forage was 6.1% on the range grazed by the herded sheep and 8.4% on the range grazed by the unherded band. These values are close to the 7% average use recorded on alpine ranges in Colorado by Paulsen (1960).

Only alpine mat clovers received more than light use and this plant group was the most important forage. Grasses and graminoids were less used than mat clovers but more than the other classes of forage. It should be kept in mind the growth form of grasses and graminoids lends itself to the detection of grazing more than does the growth form of most of the alpine forbs. Because non-cushion forbs were present when utilization was estimated it is probable utilization was underestimated for this plant group. Cushion forbs were little used. Most cushion forbs have rather low digestibility (Smith 1969) and may also be unpalatable to sheep.

The exclosures allowed the influence of protection from grazing on the vegetation to be determined. A general increase in total plant coverage inside the exclosures was accompanied by a distinct change in plant composition. The most important changes were the decrease in canopy coverage of alpine mat clovers when protected from grazing and an increase in the canopy coverage of non-cushion forbs.

Alpine mat clovers are very well adapted to sheep grazing, as are cushion forbs; however, in contrast to the mat clovers, this plant group was little utilized. Non-cushion forbs and geum generally showed an increase in coverage when protected from grazing. Grasses and graminoids did not change coverage under protection and also maintained their coverage under grazing.

Total plant coverage was either increased or at least maintained under both grazing management systems, and it is not possible to recommend one system over the other from the standpoint of the vegetation. Both systems provided levels of forage utilization that appear to be within allowable limits. Nor were there any strong differences in the weight gains of lambs grazed under the two systems. It appears that other factors, such as the

availability of herders or economics, may have to be used to select a grazing system on alpine sheep range.

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APPENDIX

Alphabetical list of scientific¹ and common names² of taxa collected.

Grasses

<i>Agropyron scribneri</i> Vasey	Scribner wheatgrass
<i>Agropyron trachycaulum</i> (Link) Malte	Slender wheatgrass
<i>Agrostis idahoensis</i> Nash	Idaho bent
<i>Deschampsia caespitosa</i> (L.) Beauv.	Tufted hairgrass
<i>Festuca occidentalis</i> Hook.	Western fescue
<i>Festuca ovina</i> L.	Sheep fescue
<i>Festuca rubra</i> L.	Red fescue
<i>Hesperochloa kingii</i> (S. Wats.) Rydb.	King spikefescue
<i>Koeleria cristata</i> (L.) Pers.	Prairie junegrass
<i>Poa</i> L.	Bluegrass
<i>Poa alpina</i> L.	Alpine bluegrass
<i>Poa cusickii</i> Vasey	Cusick bluegrass
<i>Poa rupicola</i> Nash	Timberline bluegrass
<i>Trisetum spicatum</i> (L.) Richt.	Spike trisetum

Graminoids (sedges and woodrush)

<i>Carex albonigra</i> Mack.	Blackandwhitescaled sedge
<i>Carex aquatilis</i> Wahl.	Water sedge
<i>Carex bigeovii</i> Torr.	Bigelow sedge
<i>Carex ebenea</i> Rydb.	Ebony sedge
<i>Carex elynoides</i> Holm.	Blackroot sedge
<i>Carex obtusata</i> Lilj.	Obtuse sedge
<i>Juncus</i> L.	Rush
<i>Luzula spicata</i> (L.) DC.	Spike woodrush

Cushion Forbs

<i>Antennaria microphylla</i> Rydb.	Littlehead pussytoes
<i>Antennaria rosea</i> (D.C. Eat.) Greene	Rose pussytoes
<i>Arenaria congesta</i> Nutt. ex T. & G.	Ballhead sandwort
<i>Arenaria obtusiloba</i> (Rydb) Fern.	Twinflower sandwort
<i>Arenaria rubella</i> (Wahlenb.) Smith	Sandwort
<i>Eritrichium nanum</i>	
var. <i>elongatum</i> (Rydb.) Cron.	Alpine forgetmenot
<i>Phlox caespitosa</i> Nutt.	Tufted phlox
<i>Phlox multiflora</i> A. Nels.	Flowery phlox
<i>Phlox pulvinata</i> (Wherry) Cron.	Mat phlox
<i>Sedum lanceolatum</i> Torr.	Lanceleaf stonecrop
<i>Silene acaulis</i> L.	Moss silene

Mat Clovers

<i>Trifolium dasyphyllum</i> T. & G.	Whiproot clover
<i>Trifolium nanum</i> Torr.	Dwarf clover

Non-Cushion Forbs

<i>Achillea lanulosa</i> Nutt.	Western yarrow
<i>Agoseris glauca</i> (Pursh) D. Dietr.	Pale agoseris
<i>Androsace septentrionalis</i> L.	Pygmyflower rockjasmine
<i>Anemone patens</i> L.	Spreading pasqueflower
<i>Arnica fulgens</i> Pursh	Orange arnica
<i>Arnica latifolia</i> Bong.	Broadleaf arnica
<i>Artemisia scopulorum</i> A. Gray	Alpine sagewort
<i>Aster alpigenus</i> (T. & G.) A. Gray	Aster
<i>Aster alpinus</i> L.	Alpine aster
<i>Aster foliaceus</i> Lindl.	Leafybract aster
<i>Astragalus alpinus</i> L.	Alpine astragalus
<i>Besseyia wyomingensis</i> (A. Nels.) Rydb.	Wyoming kittentails
<i>Calochortus</i> Pursh	Mariposalily
<i>Campanula uniflora</i> L.	Singleflower bellflower
<i>Castilleja rhexifolia</i> Rydb.	Splitleaft indianpaintbrush
<i>Castilleja sulphurea</i> Rydb.	Sulfur indianpaintbrush
<i>Cerastium arvense</i> L.	Starry cerastium
<i>Cirsium polyphyllum</i> (Rydb.) Petr.	Manyleaved thistle
<i>Claytonia lanceolata</i> Pursh	Lanceleaf springbeauty

Crepis nana Richards.
Crepis runcinata (James) T. & G.
Delphinium nelsonii Greene
Dodecatheon conjugens Greene
Dodecatheon radicans Greene
Draba spectabilis Greene
Epilobium alpinum L.
Erigeron compositus Pursh
Erigeron simplex Greene
Erigeron ursinus D.C. Eat.
Eriogonum flavum Small
Galium boreale L.
Geum rossii (R. Br.) Ser.
Geum triflorum Pursh
Habenaria dilatata (Pursh) Hook
Lewisia pygmaea (A. Gray) Robins.
Lomatium montanum C. & K.
Lupinus monticola Rydb.
Mertensia alpina (Torr.) G. Don
Mertensia ciliata (James) G. Don
Myosotis alpestris Schmidt
Oxytropis parryi A. Gray
Pedicularis goenlandica Retz.
Pedicularis parryi A. Gray
Penstemon procerus Dougl.
Phacelia Juss.
Polemonium viscosum Nutt.
Polygonum bistortoides Pursh
Potentilla diversifolia Lemn.
Ranunculus pygmaeus Wahl.
Rumex acetosa L.
Sagina saginoides (L.) Britt
Saxifraga rhomboides Greene
Sedum rhodanthum A. Gray
Senecio fremontii T. & G.
Sibbaldia procumbens L.
Solidago ciliosa (A. Gray) A. Nels
Taraxacum officinale L.
Trifolium parryi A. Gray

Tiny hawksbeard
 Dandelion hawksbeard
 Nelson larkspur
 Sailorscap shootingstar
 Southern shootingstar
 Showy draba
 Alpine willowherb
 Fernleaf fleabane
 Oneflower fleabane
 Bearriver fleabane
 Yellow wildbuckwheat
 Northern bedstraw
 Alpine avens
 Threeflower avens
 White bogorchid
 Least lewisia
 Mountain lomatium
 Lupine
 Alpine bluebells
 Mountain bluebells
 Alpine forgetmenot
 Parry loco
 Elephanthead lousewort
 Parry lousewort
 Littleflower penstemon
 Phacelia
 Sticky polemonium
 Americanbistort knotweed
 Platte cinquefoil
 Pygmy buttercup
 Garden sorrel
 Arctic pearlwort
 Diamondleaf saxifrage
 Rosecrown stonecrop
 Fremont groundsel
 Sibbaldia
 Fringed goldenrod
 Common dandelion
 Parry clover

Shrubs

Dryas octopetala L.
Potentilla fruticosa L.
Ribes cereum Dougl.
S. reticulata ssp. *nivalis* Hook.

White mountain dryad
 Shrubby cinquefoil
 Mountain gooseberry
 Nettleleaf willow

¹Scientific names follow Harrington (1954).

²Common names follow Beetle (1970).



Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

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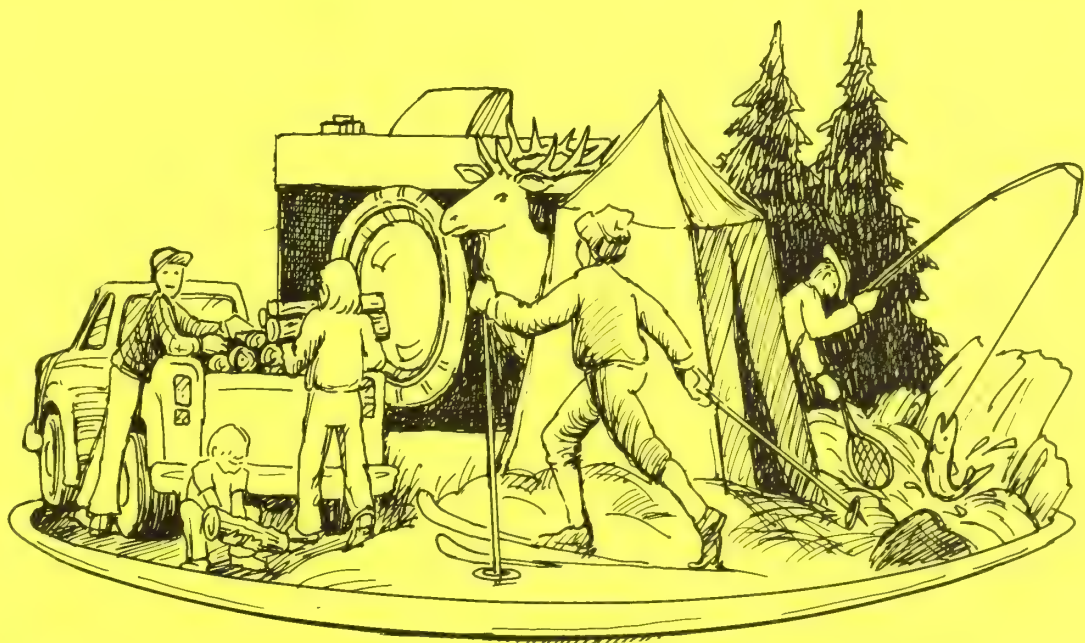
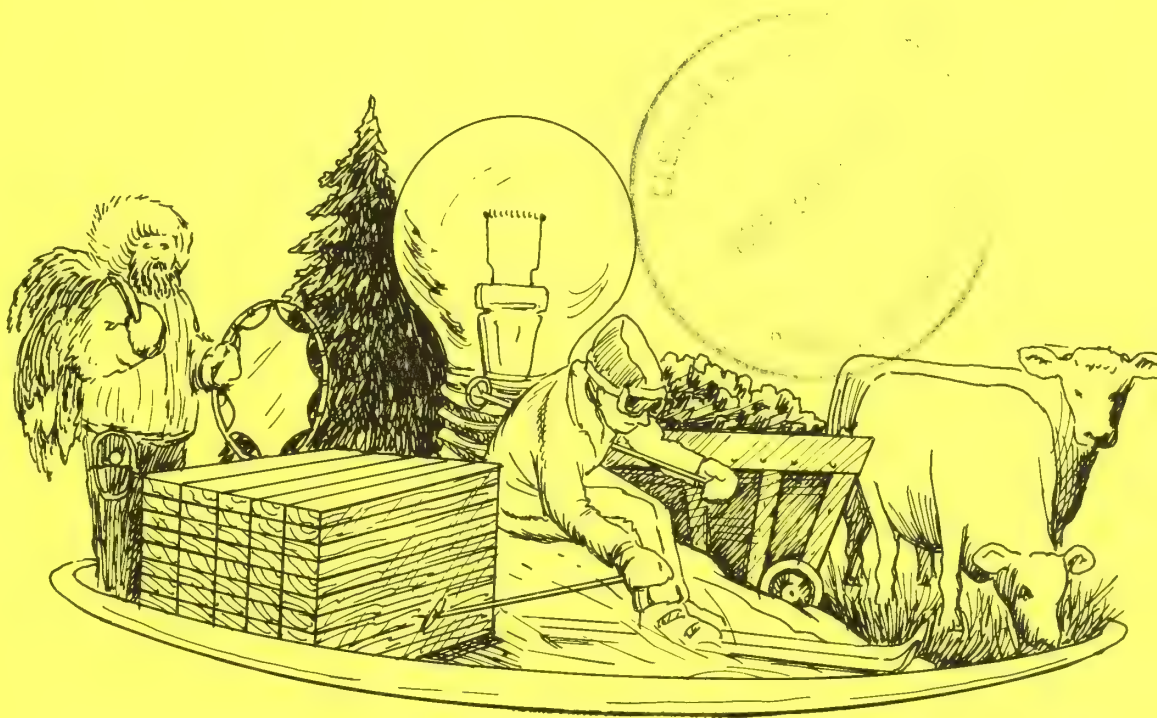
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General Technical
Report RM-148



Toward the Measurement of Total Economic Value

George L. Peterson and Cindy F. Sorg



Abstract

Considerable progress has been made in recent years in the valuation of non-priced goods. However, emphasis has been on those things most readily measurable. Valuation of wildlife benefits, for example, has aimed at consumptive, on-site recreation use (i.e., hunting and fishing). The danger in these partial estimates of value is that measuring only the on-site consumptive use of wildlife may presume to measure total value. This report examined the task of measuring off-site non-consumptive wildlife values by considering values that include: total value, option value, existence value, quasi-option value, and bequest value. Discrepancies in definitions, measurement problems, and research needs are addressed in this collection of papers.

Toward the Measurement of Total Economic Value

George L. Peterson and Cindy F. Sorg¹

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Toward the Measurement of Total Economic Value

George L. Peterson and Cindy F. Sorg

In a free economy there are three ways to decide how to allocate resources. One is market equilibrium; another is political equilibrium; the third is benefit cost analysis (BCA). In the first method, people bargain with each other to exchange goods and services within a framework of established economic rights and rules. The second method is a non-violent means of collective decisions, resolving conflicts, and distributing wealth. The outcomes of markets and politics are "sovereign," because they result from free choices of individuals. The third method, benefit-cost analysis, is a technical simulation of market equilibrium that attempts to correct market imperfection resulting from failure of imperfect competition. It provides reasoned information about the economic efficiency of alternative choices.

"BCA" is used often, in some form, whenever a choice must be made. Its applications are the most formal and demanding when assessing action by government to regulate the market or to supply goods and services directly. BCA attempts to evaluate the economic efficiency of various government proposals by estimating and summing all the costs and benefits, so that the net gain in aggregate wealth with vs. without a proposal can be measured.

In theory government action is needed where externality and monopoly create inefficient market choices. A market seeks equality of the producers' marginal revenue and marginal cost -- that point at which one more unit of production earns less income than its cost. The aggregate wealth of society is greatest, however, when marginal willingness to pay equals marginal cost -- that point at which the monetary value of the benefit to society from one more unit of production equals its cost to society. The two are identical where externality and monopoly are absent and transaction costs are zero. Then, the free market serves the best interest of society by serving the best interest of each individual separately.

However, there are "slippery" goods that evade market choices, and are non-rival or non-excludable in consumption. Thus, they produce costs and benefits which are ignored by private firms and market transactions; the result is disparity between market equality and maximum aggregate wealth. Similarly benefits one at the expense of society. Therefore, by political choices, government regulates some industries and even supplies some goods and services itself.

Theoretically, the task of BCA is to specify the societal marginal willingness to pay (i.e., demand) functions and the

societal marginal cost functions, then solve the resulting set of simultaneous equations to allocate resources optimally. However, these equations have not been written. Until they are, the best that can be done is to design discrete choices and compare them by estimating their costs and benefits. Although there may be a tendency to think of these costs and benefits in terms of quantities and prices, major government action may have non-marginal consequences, making the concept of a simple price meaningless, unless it is the price of the whole change, in contrast to a common price of the different elements of change.

Market prices may be distorted by the conditions government is trying to correct, and even by the government action itself. Furthermore, government is involved because markets cannot set meaningful prices for many of the changes. Therefore government cannot make decisions using the same criteria used by private firms.

Much progress has been made in recent years in the valuation of non-priced and non-priceable goods. However, emphasis has been on those things most readily measurable. Valuation of wildlife benefits, for example, has aimed at consumptive, on-site recreational use (i.e., hunting and fishing). While the results are not without controversy, economists have estimated values for activities such as hunting and fishing. These values are consistent in independent research efforts.

The danger in partial estimates of value is that measuring only the on-site consumptive use of wildlife may presume to measure total value. Killing and eating animals or hanging them on the wall are not the only ways wild animals contribute value. For example, people visit zoos, attend wildlife movies, and buy books about wild animals. Viewing animals in their natural habitats provides enjoyment for many people, and is a major attraction to some national parks. This is a cost which may suggest some value(s), but is not a value itself. This is done for reasons closer to being or suggesting values than the costs are.

There are two ways to include nonconsumptive values in the decisionmaking process. One is through political action. The other is to devise ways to measure them scientifically and include them in BCA. If these other values are not included in BCA, the results of BCA are incomplete, and the conclusions invalid. However, there is not unanimous agreement that such values are measurable. Some would argue that the best we can do is show the consequences and let the political system reach its own conclusions. However, because BCA is widely used to evaluate public projects, it is imperative to attempt to measure and include the nonconsumptive values.

This report examines the task of measuring off-site non-consumptive wildlife values. Alan Randall discusses "The Total Value Dilemma." Any proposed action affecting the supply of wildlife may affect several components of demand. A given individual may have several different objectives or concerns related to the change in wildlife. These concerns generate willingness to pay (or compensation demanded) for the change. Can the separate components of value be identified and measured independently, or is it more meaningful to measure the total value of the change? Evaluation of some management actions may require separation of the components. Also, there may be instances where the off-site non-consumptive values may be dominant in a given decision. Randall develops a conceptual framework for defining and estimating total value.

David Brookshire, Larry Eubanks, and Cindy Sorg look at "Existence Values and Normative Economics" by first noting discrepancies in definitions and measurements of existence value within and across research studies. Then they consider whether the nature of the values conflicts with the normative base of the benefit-cost framework regardless of consensus in terminology. Perhaps elements of existence value are based upon non-efficiency considerations, and, therefore, are not conducive to a BCA criterion.

V. Kerry Smith discusses "Intrinsic Values in Benefit Cost Analysis." He argues that option, existence, and bequest value are concepts consistent with established models of consumer choice, but suggests the theoretical framework is not well-developed, and there is consequent possibility to ignore such values or to exploit them in the justification of proposals. Smith defines these components of value and shows where they fit in modern consumer theory. He also discusses the prospects for measurement and explores the policy implications.

In the last paper, Richard Bishop concentrates on uncertainty in resource valuation. He reviews the theoretical literature on option value as a guide for empirical research. Bishop examines the theoretical definitions needed to allow measurement of welfare change under uncertainty with emphasis on "option price" and "quasi-option value."

Some progress has been made here toward a consistent

theoretical framework that integrates elusive components of value into the general theory of economic efficiency. More theoretical refinement is needed, and the move towards collection of empirical data will be difficult. Much research is needed before estimates of option, existence, and bequest value can enjoy the same credibility as market prices or even on-site values measured by travel cost analysis and the Contingent Value Method.

Major effort is needed in at least four areas. First, the concepts need to be part of a consensus of economic theory. The kinds of values and observation processes involved need to be clearly defined. Second, the objects to which value is to be assigned need to be defined better. Value greatly depends on the context. "Existence value" is only a partial term; the phrase "existence value of - - - -" needs to be completed.

Third, more knowledge is needed about how people perceive and think about things. Economic value is a concept of exchange under threat of exclusion (i.e., an inherently market phenomenon). It depends on (1) the strength of the individuals' "value" on the function performed, and (2) the "value" in exchange as determined by the market context. It may be difficult for people to think in market terms about things they have never experience in that context, or things that inherently cannot be experienced in a market context of exchange and exclusion. To get a valid response, economists should draw upon other disciplines, especially psychology.

Fourth, an empirical history is needed. Certification of reliability and validity in the measurement of things such as option, existence, and bequest value require proven performance. Empirical experience, in turn, can lead to adoption of standard units and standard methods, further enhancing ability to make comparisons and generalizations.

From a broader perspective, economic efficiency, as defined in terms of micro-economic consumer theory, is normative and somewhat narrower. The extent to which scientific measurement of total value is used to make decisions will be determined by the political system. However, it should be determined whether those components of value can be measured, whether or where their magnitudes are significant, and whether decision processes are sensitive to these facts.

The Total Value Dilemma

Alan Randall¹

Abstract--Total value may be measured directly, or component-by-component. The first-mentioned approach restricts estimation techniques to the contingent valuation method, while the second allows a wider range of estimation methods but encounters conceptual difficulties in formulating the relationship between total value and component values. This dilemma is elaborated, and some partial solutions are suggested.

The total value of some environmental asset can be estimated directly, using the contingent valuation method. The one-shot estimate of total value will be acceptable for benefit cost analysis, if reliable contingent valuation methods (CVM) can be designed and implemented. However, one-shot estimation of total value via non-CVM methods does not appear feasible.

Another approach to determining total value is to identify its components, estimate the value of each component using appropriate methods, and sum the component values according to rules consistent with the theoretically valid relationships among value components. This may permit use of estimation methods (such as the travel cost, property value, and hedonic methods) that use data obtained from transactions in markets for related goods and services to estimate benefits for some components of total value. For value components that can be estimated with CVM and non-CVM methods, there is the opportunity for validation by cross-technique comparison of results.

However, the "taxonomy of value components" approach encounters special difficulties. First, various inconsistencies and unresolved problems limit development of a coherent taxonomy of value components.² Without a coherent taxonomy, it is impossible to estimate correctly total value by summing the component values. Second, many of the value components that are identified in various taxonomies (e.g., existence value, option price, off-site or vicarious user values) are difficult to estimate using non-CVM methods. The "taxonomy of value components" approach allows non-CVM estimation methods-- for exclusive use, or for corroboration of CVM

results -- for only some of the important value components, such as on-site use value. For other value components and for total value, CVM benefit estimates cannot be corroborated by estimates made with other methods.

This is the total value dilemma. Total value may be estimated directly by CVM; but this eliminates corroboration using other methods. On the other hand, the "taxonomy of value components" approach permits use of non-CVM methods for components; and valid summation of component value estimates to obtain total value will be impossible until a valid taxonomy is developed.

Reliance on CVM may not be as undesirable as once believed. There has been a greater recognition of the analytical difficulties in the non-CVM (e.g., weak complementarity or hedonic price theory) methods, while evidence that CVM is "working fairly well" has been accumulating.³ Further, recent theoretical analyses suggest that it is possible to construct satisfactory CVM benefit estimators (Hoehn and Randall 1987). The imperative to use the "taxonomy of components" approach because it avoids total reliance on CVM is not as strong as it once was.

For some components of value (e.g., existence value and off-site or vicarious user value), there may be more opportunities than currently recognized for generating value-relevant information via methods other than CVM. Corroboration of CVM results with evidence generated independently of the CVM exercise may be possible in some broad classes of situations.

A Definition of Total Value

Consider an environmental asset capable of producing a time-stream of a single service $Q(t)$, $0 \leq t < \infty$, where t indi-

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²For example, Schmalensee (1972), Graham (1981), Bishop (1982), Bishop, (this volume), and Smith (this volume).

³For example, Randall et al. (1983), and Cummings et al. (1986).

cates time. If $V(t)_0$ is the aggregate value (across people) of $Q(t)$, as anticipated at $t = 0$, the present value of this asset at that time is:

$$P_0 = \int_0^{\infty} V(t)_0 e^{-rt} dt, \quad [1]$$

where r is the rate of discount. P_0 can be interpreted as the value that would be lost if this asset were destroyed at $t = 0$, or as the present value of the "without project" option when evaluating some proposal to modify the environmental asset and its subsequent time-stream of services.

Individual valuations, $V_i(t)$ -- which are summed, unweighted, across all affected individuals to calculate $V(t)$ -- emerge from the individual solutions to constrained choice problems.

Suppressing i and t , the individual maximizes utility,

$$U = f(Z) \quad [2]$$

where Z is a vector of activities that yield satisfaction.

The concept of activity is broadly defined, and includes work and other income-generating activities, formal educational activities, reading and watching television and movies (which may have an educational or informational component), eating, household maintenance, hobbies, and recreational activities (including sports, physical exercise, hiking, nature study, sightseeing, etc.).

These activities are produced by the household, in a process which combines purchased good and services, environmental amenities and other public good, and the household's time effort. This production process is governed by the household's activity production technology.

A household production function for activities using a natural resource amenity is represented as:⁴

$$Z = g(X, Q | T) \quad [3]$$

where

X = a vector of goods and services other than the specific natural resource Q ; and

T = the household's production technology.

By minimizing expenditures, PX (where P is a vector of prices for commodities X), subject to (i) $U = f(Z) \geq U^0$, the level of satisfaction enjoyed when Q is at its initial level Q^0 and (ii) the activity production function (3), one obtains the expenditure function $E^0(P, Q, U^0)$. The first derivative of the expenditure function with respect to Q yields an inverse compensated demand function for Q :

$$\frac{dE^0}{dQ} = -E_Q^0(P, Q, U^0). \quad [4]$$

⁴In this formulation, the household's time contributed to producing activities is not explicitly introduced, because we make no subsequent use of that variable. In analyses performed for other purposes, (e.g., study of the work-leisure choice), this time variable is often a major focus.

The total value of Q^0 to the individual is

$$V = - \int_0^{Q^0} E_Q^0(P, Q, U^0) dQ. \quad [5]$$

Aggregating V across individuals at each time, discounting, and integrating across time, the total value of the environmental asset (1) is obtained.

Several complications are implicit in this formulation of environmental asset values. First, current values $V(0)$ are only a minor portion of the time-stream of values $V(t)$; the remaining values will accrue in the future only. Thus, $V(t)_0$ is the present anticipation of $V(t)$. New information will be introduced at various times, causing anticipations to change. This phenomenon is accepted in asset-pricing theory, where the "efficient markets hypothesis" posits that, at any time, the price of an asset reflects all of the information currently available to market participants. For non-marketed environmental assets, however, the decentralized generation and processing of information envisioned in the "efficient markets hypothesis" is absent. Special efforts are necessary to ensure that $V(t)_0$ incorporates adequate intelligence about future demand and supply conditions that affect $Q(t)$. Alternatively, analysts could pay more attention to gathering and processing information about citizens' current expectations of future environmental services values.

Second, neither the utility function (equation [2]) nor the activity production function (equation [3]) places any prior restrictions on the kinds of activities that may generate utility and value. These include current observable on-site use values, where Q is combined with purchased commodities such as travel, accommodation, and complementary equipment; most economists focused initially on these sources of value. However, total value may also include off-site or vicarious uses, the anticipation of future use, and the value obtained from the simple knowledge that the asset continues to exist.

Third, the activity production function depends on the household's activity production technology, which is subject to augmentation or degeneration over time. The activity production technology at any given time is a function of the activities produced at previous time. Thus, it may be represented as:

$$T_t = h(Z_{\tau}(X_{\tau}, Q_{\tau} | T_{\tau}))$$

$$\text{for all } \tau \text{ in } 0 \leq \tau < t. \quad [6]$$

This explicitly recognizes the development of skill in activity production through conscious acquisition of information and instruction and through the less deliberate process of "learning by doing." Past activity production influences the capacity to achieve satisfaction from current activities. Given the nature of the processes by which activity production technology is acquired, it is immediately clear that T may differ

substantially across households, as well as over time in a given household.⁵

A clearer understanding of how technology is developed may clarify the relationships between on-site or "hands-on" use, vicarious use, and enjoyment that depends only on the existence of the environmental asset.

Components of Total Value

The total value of an environmental asset may be defined as in equations [1-5]. In the absence of well-functioning markets for environmental assets, contingent valuation seems to be the only feasible method for estimating total value in a one-shot analysis.

An alternative approach is to attempt a taxonomy of the components of total value, estimate each component using appropriate methods, and sum the component values to determine total value. If the taxonomy is complete and internally consistent, and if estimation methods exist that are appropriate for each of the value components, this approach would permit accurate estimation of total value. It would have the advantage of reducing reliance on a single valuation technique (contingent valuation) because some components of total value are amenable to estimation with other kinds of methods. For some components of total value, cross-technique comparisons may provide evidence about the quality of benefit estimates.

However, the better-known taxonomies of value components were not developed from the outset with systematization in mind. For example, initial successes in establishing the reputability of the travel cost method of valuing on-site recreational uses led some to wonder whether there might be other kinds of value -- vicarious use value, option value, existence value, and/or preservation value -- that were being ignored. Various additional categories of value were proposed and soon the literature was awash in controversy as to whether particular categories of value were scientific (in the sense that they were subject to the rules of evidence common to scientific endeavor) and whether the various categories of value that had been proposed were mutually exclusive. Was it possible, or likely that some of the proposed categories of benefits, when carefully defined so as to avoid double-counting, could be of zero or negative value?

By now, we have reached a stage where relatively complete taxonomies of value components have been proposed, and considerable progress has been made in clearing up controversies about the mutual exclusivity of value components and the possibility that some components may take negative values. The following taxonomy is reasonable representative of the current state-of-the-art.

⁵Stigler and Becker (1977) have argued that the concept of activity production technology is of great potential fruitfulness in explaining differences in activity choice among households. If, as they claim, T is analytically more tractable than the process of preference formation, an appropriate research strategy would focus on T while essentially ignoring tastes and preferences.

Use Value

In general, any activity produced in a process such as that defined in equation (3), in which Q is combined with one or more elements of the X vector, may generate use values. Where Q and some element, X_j , of the X vector are weak complements in production of a particular activity, it is in principle possible to estimate the use values associated with that activity by analyzing data generated by transactions in the market for X_j . The weak complementarity approach has been useful in evaluating benefits generated by on-site use. Weak complementarity between travel services and destination site quality provides the basis for the travel cost method of valuing recreation amenities, while use values for location-specific amenities are often estimated by analyzing the housing and labor markets. For these cases, the researcher is not confined to contingent valuation methods which allows those who prefer other kinds of methods to use them.

On-site recreation benefits and the value of amenities associated with places of residence and work are only a few of the use values generated by environmental assets. Others include incidental use, such as viewing scenery while traveling for a different purpose; off-site use such as looking at pictures, descriptions and accounts made available through various media; and non-participant or vicarious uses, such as another person's environment-related activity. Although these kinds of on-site uses are important, they do not readily generate information about participation rates or user values.

In summary, those applications of the weak complementarity approach that are commonplace are nevertheless confined to a mere subset of use values.

It is necessary to distinguish among four classes of use values, on the basis of the timing of the use decision (past or future), the uncertainty that attaches to future use, and the value that attaches to delaying irreversible decisions about use if new information is expected to become available later.

Past and Current Use Values are observable ex post (i.e., after the use decision has been made). For certain kinds of use (including several that are frequently researched), ex post use is routinely recorded and amenable to valuation methods founded upon the assumption of weak complementarity.

Expected Value of Future Use.--Future use is ex ante (i.e., the irrevocable use decision is yet to be made), uncertain, and subject to change as new information becomes available. Future use must be projected from past use or inferred from, for example, survey data stating the ex ante intentions of the identifiable user population. The expected value of future use -- often called "expected surplus" -- may be projected from studies (including those that apply weak complementarity techniques) of ex post use values, or estimated in CVM studies of ex ante use. In another article in this report, Smith points out that the welfare analytics of ex post and ex ante use value are fundamentally different, and these differences should lead to different empirical estimates (or, more precisely, empirical estimates of different constructs). Applied procedures that estimate the stream of future benefits generated by an envi-

ronmental resource (a fundamentally *ex ante* concept) by adding *ex post* and *ex ante* estimates of various components of value, therefore, are internally inconsistent.

(Ordinary) Option Value.--If uncertainty attaches to the future availability of the environmental asset, a risk-averse household may be willing to pay a premium beyond expected surplus (ES) to ensure future availability. This premium has been called "option value" (OV). However, the total willingness to pay, now, for an option for future use is called "option price" (OP), defined so that $OP = ES + OV$. There has been considerable controversy (Schmalensee 1972) as to whether OV may take a negative value, in contrast to the positive value assumed by early writers such as Weisbrod (1964). The problem is that there are two kinds of risk: demand risk, in which a purchased option would prove useless if future demand did not eventuate; and supply risk, in which future availability is not assured unless the option is purchased. In buying an option, one may encounter demand risk as a result of an act taken to avoid supply risk. Only in the case where demand is certain and supply uncertain can we be assured that, for a risk averse household, $OV > 0$ and $OP > ES$ (Bishop 1982).

These constructs (ES, OV and OP) are all based on the notion of sure payments. Building upon the literature on the economics of insurance, Graham (1981) has shown that some schemes of *ex post* contingent payments may generate values greater than the larger of OP and ES. Graham defines the "fair bet point" (FB), which always has an expected value equal to or greater than OP.

It seems clear that FB is the ideal construct for valuing future use under uncertainty. OP can be viewed as the second-best construct, because it is the value that emerges in the absence of perfect contingent claims markets.

Neither FB nor OP is directly observable. Both could be estimated via CVM; but, the complex notion of contingent claims markets that is fundamental to FB might not be effectively communicated to CVM respondents. This suggests a pragmatic emphasis on estimating OP via CVM, at least until experiments in estimating FB via CVM have been reported.

A second-best approach is to project ES from *ex post* use data, perhaps from analyses using weak complementarity approaches, and estimate OV in a separate exercise. OV can presumably be estimated only via CVM. Freeman (1984) suggests that OV usually will be quite small. If so, a third (and yet less desirable) approach is merely to estimate ES and use it as an approximation of future use values. Note that these second and third approaches incorporate the error (discussed in Smith's article in this volume) of confusing and/or admixing *ex ante* and *ex post* value constructs.

Quasi-Option Value.--Arrow and Fisher (1974) and Henry (1974) introduced the concept of quasi-option value, which has special pertinence to preservation vs. development decisions. If development is irreversible (e.g., preservation in period 1 allows the choice of preservation or development in period 2, but development in period 1 pre-ordains develop-

ment in period 2) and new information about the value of preservation is likely to emerge after period 1 but before the period 2 decision must be made, quasi-option value is positive. It is, essentially, the value of the emerging information conditional on having made the period 1 choice (preservation, in this case) that maximizes the period 2 array of alternatives (Hanemann and Fisher 1984).

The literature does not include empirical estimates of quasi-option value; but Hanemann and Fisher (1984) provide some numerical examples that suggest that quasi-option value may be quite large (and incidentally, much larger than ordinary option value) where preservation is an alternative to irreversible development.

The distinction between ordinary option value and quasi-option value has been the subject of considerable confusion in the literature. The Appendix of this paper offers one more attempt to clarify these concepts.

Existence Value

Value may be generated simply by knowing that the environmental asset exists. Use value is defined as any value that emerges from activities produced by combining Q and any element of X. Existence value must be generated by activities produced by the process

$$Z = g(O, Q | T) \quad [7]$$

which is a special case, in which $X = O$, of the process in equation [3]. That is, existence values for Q are generated by Q alone, subject to an activity production technology (T) which permits an understanding and appreciation of Q. No elements of the X vector are involved in the current time period. However, activities combining Q and X in some previous time periods seem essential to the acquisition of the kinds of T which permit existence activities (eq. [6]).

Pure existence value excludes any values that arise from current use or anticipated future use. Because vicarious consumption is a kind of use, all pure existence demands must be altruistically motivated. One can conceive of "interpersonal altruism" which would generate existence values from knowing Q was available for others to use; "intergenerational altruism" from knowing Q will be available for future generations; and "Q-altruism," in which the household enjoys the feeling that Q itself is benefiting from being undisturbed. The last two kinds of altruism generate "bequest values" and "intrinsic values," respectively, which are categories of existence value. Note that this discussion of various altruistic motives for existence value is not predicated on any assumption that different motivations have different observable consequences. Rather, it is intended merely to point out that there are several common human motivations that could lead to positive existence values.

Randall and Stoll (1983) offered some observations about the nature of existence value. Existence services have most all of the characteristics of other economic goods except ready

marketability. One can conceptualize a demand for, and a supply of, existence. Existence is best treated not as a discrete phenomenon (it exists or it does not), but as a continuous phenomenon (there exists more or less of some particular Q). Because supply and demand may well be continuous functions, it makes sense to distinguish between total existence value and existence value at the margin.

It follows that many kinds of goods and services have potentially significant existence values, at least in total. For commonplace goods and services, proposed projects seldom significantly reduce the supply of existence and, thus, threaten only trivial losses in existence value. Existence values are not confined to unique environmental amenities threatened with irreversible destruction. For that matter, existence values are not confined to environmental amenities at all. They occur for human artifacts and cultural manifestations, (e.g., historic buildings, grand opera, and Navajo rug weaving). Uniqueness and the threat of irreversible loss, however, are circumstances in which the incremental loss of existence values are likely to be greatest.

Existence is not only a global phenomenon. It is perfectly reasonable that the extirpation of some environmental or cultural asset from a local region would cause locally important losses of existence value, and may even be lamented in distant places.

Existence value, by definition, must be generated in processes that use Q, but not in combination with any element of the X vector, subject to an activity production technology. Nevertheless, it seems that some kind of past use is not only permissible but strictly necessary to the generation of significant existence values. Without some kind of past use, how could the technologies that permit knowledge, understanding, and appreciation of Q arise?

As environmental assets are discovered and used, through either on-site or "hands on" experiences or exposure to descriptions, representations or accounts, the technology relevant to existence activities is likely to be augmented. Existence demands, therefore, would be expected to increase for some time following discovery. This would not always be true of existence value at the margin, because there are conceivable cases in which use experiences would shift perceived existence supply sharply rightward, as what was once newly discovered comes to be recognized a commonplace.

In addition to activity production technology, the role of information about existence supply seems crucial to the determination of marginal existence values.

The processes of discovery and learning, as new information becomes available and activity production technologies are augmented, introduce a substantial volatility into total and marginal existence values. Randall and Stoll (1983) discuss the case of the snail darter. Until its discovery in 1973, its existence demand was zero. Its existence demand rose rapidly as it was accepted as a separate species and listed as endangered, and as knowledge of its existence and its plight spread rapidly among the public. Given its limited supply, it acquired a substantial marginal existence value. More recently, snail

darter populations have been found in some streams where they were previously unknown, shifting the perceived supply to the right and, presumably, reducing the existence value of the marginal snail darter. It is important to realize that this volatility of existence value has nothing to do with measurement error or bias. It is not that "the estimates" are volatile; the problem is that the perceived reality of existence value is volatile, especially when relatively large amounts of new information may be added to a small initial information base.

It is readily apparent that, of the established techniques of non-market valuation, only CVM offers any hope of estimating existence value.

Approaches To Estimating Total Value

The "taxonomy of components" approach would suggest that total value should be determined by summing the results of independently estimated current use values for all uses, option price, quasi-option value (if relevant), and existence value. Estimation methods based on weak complementarity or hedonic price theory are obvious candidates for estimating the values that emerge from those kinds of uses that are on-site and require travel or are location-specific to the place of residence or work. Further, these kinds of methods may permit projection of expected surplus from future use, which may be a serviceable approximation of option price, itself perhaps a serviceable approximation of the "fair bet point." For all other components of total value, it seems that the broad class of contingent valuation methods offer the only present real hope of value estimation. These value components include many kinds of use values, in addition to the more obvious cases of option price (or option value if expected surplus is otherwise estimated) and existence value. Corroboration of CVM value estimates with estimates obtained using other methods is infeasible in these cases. Further, for many of these cases, there seems little hope of obtaining independently-generated evidence that these values are real and positive.

An alternative approach is to attempt one-shot estimation of total value via CVM. It is relatively simple to convey the notion of total value to a CVM participant, pointing out that all current use values (including the informal, off-site, and vicarious), future use values and existence values are to be considered. However, there seems to be much subtlety inherent in any taxonomy of value components. The distinction between vicarious use value and existence value, and the precise definition of option value would seem to place considerable responsibilities of communication upon the designer of a CVM exercise, the interviewer or experimenter, and the citizen participant.

The following, more elaborate, approach may serve to enhance credibility of benefit estimates among the widest possible audience. Estimate total value via CVM. Where major categories of current use value are amenable to estimation via weak complementarity and hedonic price theory approaches, and the resulting estimates can be used to project

future use values, these approaches should also be implemented. Two kinds of corroboration would then be possible. These same categories of value could also be estimated via CVM, allowing direct tests of comparability. As long as the CVM estimate of total value exceeds the estimates (obtained by any and all methods) of major categories of current and future use value, the CVM estimate of total value can be taken as a lower bound on total value. This follows from two observations: (1) important positive components of value are included in one-shot total value but not in the estimates of specific categories of use values; and (2) CVM formats can be designed that seem to be immune to overestimating total value.

Is CVM a Satisfactory Benefit Estimator?

Estimation of total value will require considerable reliance on contingent valuation. Avoidance of CVM seems certain to result in the omission of important components of total value. For this reason, it is important to summarize here some recent results pertaining to the satisfactoriness of CVM as a benefit estimator (Hoehn and Randall 1987).

The issue with CVM has always been data quality. If the value data can be trusted, these data (unlike the data used in weak complementarity and hedonic price theory approaches) can be directly interpreted as theoretically valid estimates of welfare change (Bradford 1970, Randall et al. 1974, and Brookshire et al. 1980). However, CVM data are self-reported by participants in interaction with a researcher or his representatives. One concern is that various self-reporting biases, and other biases inadvertently introduced by the research design and/or the interaction between researcher and participant, may be endemic to CVM. However, much empirical evidence supports CVM, despite occasional anomalous results. The general perception among environmental economists may be summarized by the following quotation from an author who was once himself among those skeptical of CVM.

“(T) here is growing recognition that contingent valuation is turning out better than many people, including the present writer, expected... The ‘bottom line’ seems to be that, while contingent values are not precise, they are sufficiently accurate to be useful in policy analyses” (Bishop 1984 draft of his article in this report).

Hoehn and Randall (1987) take the attitude that most of the purported biases in contingent valuation are rather simple concerns that can be avoided or minimized through careful attention to research design, sampling, and administration of the experiment or survey. The two concerns that they recognize as genuinely interesting are: (1) individuals may behave strategically, misreporting their “true” valuation in order to influence the outcome of the research; and (2) individuals may treat the whole exercise as hypothetical or inconsequential, and thus devote little effort to the introspection that is necessary to discover what one’s “true” valuation really is. Hoehn and Randall analyze these issues by assuming a rational self-

seeking respondent and using simple theoretical models to predict his/her behavior when confronted with a CVM exercise.

Assume an individual -- an experimental subject or survey respondent -- believes the results of the valuation exercise will influence policy. Assume also that the individual perceives that she is a member of a sample of citizens participating in the exercise. Does she “take it seriously?” It is reasonable to assume she will take it at least as seriously as voting in elections or participating in a political poll (where, again, her influence is magnified because she is a member of a sample chosen to represent a larger population).

Now, assume that formulating (“figuring out”) her WTP/ WTA for specified changes in Q (or, even more difficult, specifying her total value curve) is not so simple a task that it can be accomplished instantaneously and without cost. The choices offered in the contingent market seldom are familiar and routine, even with the best research design. There is a positive relationship between the effort she invests in value formulation and the precision of the value at which she arrives. If the value formulation task is very difficult and/or the individual limits the effort she invests therein, she may solve the value formulation problem incompletely or imprecisely.

This places in perspective the difference between contingent markets and “real” markets. First, the goods offered in contingent markets are not always familiar, and individuals may not associate these particular goods with trading possibilities. Unfamiliar goods are often introduced in “real” markets and, especially, in market experiments. So, this distinction between “real” and contingent markets is, if anything, a matter of degree. Second, the penalty for a wrong decision may be substantial in “real” markets; your money is gone and you are left with some purchase that has disappointed you. However, there is a penalty for a wrong decision in a contingent market; one’s opportunity to influence policy is wasted or misused. Again, the distinction between “real” and contingent markets is, if anything, a matter of degree.

If value formulation is imperfect in contingent markets, the formulated values would include some error. If valuation is performed in the Hicksian compensating framework (i.e., WTP for increments in Q and WTA for decrements), imperfect value formulation would lead to understatement of WTP and overstatement of WTA.⁶ At least, we know the direction

⁶The intuitive explanation of this result is as follows. In order to formulate her WTP, the participant must first solve the problem: minimize expenditure subject to utility constrained at the initial level. Imperfect solution of that problem can have only one kind of outcome, the identification of some expenditure larger than the minimum. This overestimation of minimum expenditure must lead the participant to underestimate her compensating surplus, WTP. Thus, any error in formulating WTP in a compensating framework would lead to its understatement.

If equivalent measures of value are sought, the results of formulation error are not so clear. There are two problems to solve: (1) the “with policy” or subsequent, utility level must be found by maximizing utility given the subsequent opportunity set; and (2) expenditure must be minimized subject to utility constrained at the subsequent level. Formulation error at stage (1) would, again overstate expenditure. The final outcome is ambiguous when equivalent measures of value are used.

of any error that incomplete value formulation would introduce; the directional effect is to understate the value of gains and overstate the value of losses. This kind of error has a conservative influence on BCA.

Now, assume the individual is not above strategic behavior, defined as reporting something other than one's formulated value in order to influence the results of the exercise in one's favor. Some participants would reject this kind of behavior on moral grounds, while others would recognize that strategic behavior is itself resource-consuming and decide not to use resources that way. Nevertheless, it is prudent to consider what kind of effect those who choose to attempt a strategic response might have on reported contingent valuation results.

To identify optimal strategies for participants, first specify the incentives that they face. For simplicity, assume that $U = U(Q, Y)$, where Y is a numeraire consisting of "all other goods." Assume the individual gains positive utility from both Q and Y . In other words, she likes Q and does not like taxes or payments that would reduce her disposable income for purchasing other goods. The key issue, then, is how her participation in the exercise is likely to influence (1) the chances that a policy to increase Q will be implemented and (2) her disposable income, if the policy is enacted. One can model a variety of alternative contingent markets, to examine how their structure affects these things. Here, some of these models for WTP are outlined; the arguments are analogous for WTA, where the effects are usually similar but of opposite sign.

1. The government will provide the increment in Q without regard to the outcome of the benefit cost analysis. The researcher will collect stated WTP from each participant at the end of the exercise. However, Q is nonexclusive and participants will enjoy the increment in Q regardless of their reported (and paid) WTP. Strategizing respondents would report zero or very low values for WTP.
2. The government will provide the increment in Q if and only if the estimated benefits for the affected population exceed the costs. The researcher never collects the stated WTP, and nor does anyone else. The participant is forever immune from bearing any of the costs. Strategizing respondents would state high values for WTP in order to increase the probability of implementing the policy.

These cases can be dismissed immediately, because they are quite false representations of the policy environment. Case (1) is of some interest, in experimental economics, as the case most likely to elicit free-ride behavior. However, it is not common policy practice to implement proposals independently of benefits and costs, and to finance them through contributions determined by self-reported WTP. Case (2) has some appeal on the surface, because in CVM practice, the researcher seldom collects WTP. However, a deeper analysis

suggests that participants realize that if the exercise is to affect policy they will eventually pay (usually through some combination of user fees, higher taxes, and higher prices) for increments in Q . The assumption that the participant is forever immune from contributing toward the costs of policy is untenable.

More relevant models of the incentives influencing behavior in contingent markets include the following cases.

3. The proposal is implemented if the estimated benefits exceed the costs; and citizens pay in proportion to stated WTP.
4. The proposal is implemented if the estimated benefits exceed the costs; and citizens pay their per capita share of the costs.
5. The proposal is implemented if a majority of citizens approves it, given that each pays her per capita share of the costs.

In each case, the participant who likes Q but dislikes bearing additional expenses must devise a strategy designed to increase the expectation that the policy is implemented, but at the least cost to her.

Optimal reporting strategies are, for cases (3) through (5):

3. Report WTP equal to or less than one's formulated WTP. Optimal reporting strategy is related to sample size. Generally, it is best to report WTP approaching one's formulated WTP, if one believes the sample is small; with very large samples, the tendency toward free-riding is stronger.
4. If one suspects one's formulated WTP is quite different to that of other citizens, exaggerate the difference so as to shift the sample mean reported WTP nearer to one's own formulated WTP. If one expects one's WTP is a little higher than the mean, report a value still higher; similarly, if one's WTP is likely to be lower than the mean, report a value still lower.
5. No strategy is individually preferred to truth-telling. If the stated per capita cost is lower than one's WTP, it is optimal to report approval; if one's WTP is lower than the stated cost, it is individually optimal to report disapproval.

In case (3), there would be a tendency to underestimate benefits. In case (4), the variance of individual WTP would be increased, widening the confidence interval around estimated benefits. If reported WTP is limited to a minimum of zero but has no upper limit, mean reported WTP might be biased upward. However, there are statistical methods for dealing with this problem. If these methods are used, total estimated benefits would be unaffected by reporting strategies.

In case (5), there is no reporting bias. Note that, in this case, the results are expressed in terms of "number of participants expressing approval/disapproval of the proposal given a per

capita cost of \$ ____." These results are not immediately interpreted as WTP. All we know is that those who approve have formulated a WTP greater than the stated cost, while those who disapprove have formulated a WTP less than the cost. Nevertheless, if (1) the sample is divided and different subsamples respond to different stated costs and (2) the data are analyzed with appropriate statistical tools (e.g., logit analysis), valid benefit estimates can be obtained. An alternative approach is to repeat the "approve/disapprove" question with the same participant, stating different levels of per capita cost. In that way, the researcher could iteratively approach the participant's indifference point, while retaining the desired anti-strategic properties of the "majority vote" format.

This conceptual analysis of the participant's likely behavior in a contingent valuation exercise, in formulating and reporting her responses, has several implications which appear to have been corroborated in empirical applications.

First, while the incentive for careful decisionmaking and truthful reporting of valuation are not as strong as in private goods markets, they are not absent in contingent valuation exercises. This suggests that carefully designed contingent valuation studies will collect a substantial body of serviceable value data, perhaps along with a minority of less reliable observations.

Second, for a fairly wide range of contingent market designs, any biases introduced in formulating and/or reporting WTP are likely to have the effect of understating it. This applies to contingent markets based on Hicksian compensating measures of value, and assumes use of appropriate statistical analyses. Following Hoehn and Randall (1987) a "satisfactory benefit cost estimator" can be defined as one that correctly identifies all proposals that would not generate a potential Pareto-improvement (PPI) while correctly identifying at least a subset of those that would bring about PPIs. It follows that any BC estimator that reliably reports WTP, (i.e. benefit), estimates no greater than their "true" values is satisfactory. Thus, a considerable class of CVM formats that are satisfactory BC estimators can be identified.

Third, contingent valuation formats vary, and their performance characteristics differ in ways that are, to some extent, predictable. Thus, the quality of contingent value data can be improved with careful attention to contingent market design. Use of Hicksian compensating value measures and referendum formats, as in case (e), are obvious ways to minimize bias in estimated benefits while ensuring that any remaining bias is toward understatement.

These recent results have important implications for the total value dilemma. The one-shot approach to total valuation relies entirely on contingent valuation. The "taxonomy of components" approach arose historically because attractive non-CVM valuation methods were developed for specific kinds of current and future use values. The "taxonomy of components" approach allows the use of these non-CVM methods where appropriate, while attempting to plug the holes and fill the gaps with CVM studies. Without some considerable reliance on CVM, total value estimation must

remain inaccessible. Further, given the disadvantages of the "taxonomy of components" approach, those who favor it must presumably believe that the opportunities it provides for estimating some value components without recourse to CVM is an offsetting advantage. Thus, any new information with respect to the reliability or satisfactoriness of CVM has important implications for the feasibility of total value estimation and the choice of approach to be taken.

Possibility of Market Corroboration for Existence and Vicarious-Use Values

The likely empirical dominance of off-site use values and existence values in the total values associated with certain well-known and unusual environmental assets creates a special urgency about establishing the contributions of these components to total value. Because of some skepticism about contingent valuation, it would be useful to develop non-CVM methods of estimating off-site use and existence values, or of independently corroborating that such values are real, positive, and substantial (Schulze et al. 1981).

Two suggestions are offered here, addressed to existence value and the kinds of off-site use values that are generated when one enjoys environmental amenities via pictures, description and accounts made available through various communications media.

In the case of existence value, the possibility of third-party observable corroborating evidence is massively diminished by the definition of existence value as those values derivable from Q when every element of the X vector is held to zero. Nevertheless, the concept of activity production technology offers some hope. Such technology must be acquired only through past use, on-site and/or off-site. Further, individuals make conscious choices as to how much they invest in the acquisition of these technologies. Some technology may be acquired passively, as a result of incidental exposure rather than conscious effort. Nevertheless, the conscious investment of effort and resources in order to acquire activity production technologies frequently may be observed. Evidence of technology could be systematically documented with some research effort. It seems reasonable that existence demands do not diminish as production technologies for existence activities are augmented. Thus, systematic evidence of technology acquisition would provide third-party verifiable evidence of positive existence values. Evidence that technology acquisition was increasing over time, similarly, would provide evidence that existence values were increasing with the passage of time.

Second, those off-site use values that rise from the enjoyment of environmental amenities via pictures, descriptions and accounts made available through the communications media are of interest per se, and because this kind of use is likely to be important in the acquisition and augmentation of existence activity production technologies. Even casual examination of the communications media suggests the very

substantial allocation of effort to describing and depicting environmental assets, both for their own sake and as essential background to various narratives, etc.

There is no inherent reason why the economics of the communications media ought to be intractable. It should be possible to estimate demands for books, magazines, films, television programs, etc., in general and to partition out the demands for articles and programs with a strong focus on particular environmental assets. There is no good reason to believe that these demands would be other than downward sloping, which suggests that the consumer's surplus enjoyed by their audience would be positive and measurable. The existence of copyright and similar laws, however, suggests that not all of the economic surplus associated with these communications is enjoyed by consumers; some of it, apparently, any be appropriated by authors, photographers, publishers, and the like. Usually, it is assumed, the subject matter has no legal rights, and is unable to extract rents. More and more commonly, however, people who have been able -- on account of their charisma, positions of power and influence, participation in activities thought exciting, or even entirely fortuitous roles as participants or bystanders at some spectacular event -- to acquire celebrity or notoriety, have extracted rents from the communications media by selling rights to their stories, interviews, etc. It is by no means idle to wonder what revenues -- given institutions that would permit it -- the "trustees" of the Grand Canyon could accrue by licensing all media representations thereof.

More formally, it ought to be possible to estimate the necessary economic relationships and calculate the economic surplus attributable to the environmental asset subject matter of these various media presentations. If there are important and policy-relevant environmental assets for which on-site use values are but a small proportion of total value, then investment in at least a few prototypical research studies of this kind is warranted.

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APPENDIX: THE DISTINCTION BETWEEN (ORDINARY) OPTION VALUE AND QUASI-OPTION VALUE

Since Henry (1974), there has been some conceptual confusion about option value and quasi-option value. The appendix attempts to clarify these concepts by constructing a well-specified problem-context and showing how option value and quasi-option value can be defined in this common context.

The Problem Context

Consider an environment that may at any time t be in either of two mutually exclusive states, preserved ($p_t = 1$) or developed ($p_t = 0$). At the outset, $p_1 = 1$, but development, should it ever occur, is irreversible. Thus $p_t = 0, 1$ and $p_{t+1} \leq p_t$.

Let $\theta_t = 1$ if the state $p_t = 1$ is demanded at time t ; and $\theta_t = 0$, otherwise. At some earlier time τ , demand at t may be uncertain and there is some expectation ($0 \leq E(\theta_t^\tau) \leq 1$) that $p_t = 1$ will be demanded. Similarly, $\varphi_t = 1$ if preservation is supplied at time t , and 0 otherwise. Of course, preservation may be supplied at time t but not chosen; that is, $\varphi_t = 1$ permits but does not require $p_t = 1$. Given that the choice of $p_{t-1} = 1$ guarantees $\varphi_t = 1$, the chooser can (by her decision with respect p_{t-1}) determine θ_t . However, future supply may be uncertain for those who are not in a position to choose the value of p in preceding periods. For them, the expectation θ_t^τ may take values:

$$(0 \leq E(\theta_t^\tau) \leq 1).$$

Subsequent analysis is simplified by restricting t to the values 1, 2.

Quasi-Option Value

In period 1, the individual does not know the magnitude of θ_2 , but she does know that she will know θ_2 when the time comes to choose the second-period allocation. That is, θ_2^1 is uncertain but θ_2^2 is known. In determining her willingness to pay (WTP) for the state $p_1 = 1$, is there a positive component that is attributable to the prospect that θ_2^2 will be known? In other words, is $p_1 = 1$ worth any more if θ_2^2 is known than if $\theta_2^2 = \theta_2^1$ and is uncertain?

The answer is "yes." The increment in value is called quasi-option value (Arrow and Fisher 1974) and has been shown (Hanemann and Fisher 1984) to be equal to the value of information about θ_2^2 conditional on $p_1 = 1$ having been chosen.

(Ordinary) Option Value

While θ_2^1 s uncertain, so is θ_2^2 ; $E(\theta_2^1) = E(\theta_2^2) \leq 1$ and nothing is learned about future demand as time passes. The period 2 use decision must be made when θ_2^2 remains uncertain. Nevertheless, an uncertain demander may be willing to pay some premium for $p_1 = 1$ because the choice of $p_1 = 1$ guarantees $\varphi_2^1 = 1$. That is, the choice of $p_1 = 1$ provides an option for $p_2 = 1$; or, to put it yet another way, increases and secures supply from $0 \leq E(\varphi_2^1) \leq 1$ to $\varphi_2^1 = 1$. What is the value of the premium?

This problem is usually addressed by assuming risk aversion. However, there are two kinds of risk. If the individual does not buy the state $p_1 = 1$, by her default φ_2^1 remains

uncertain; i.e., there is a supply risk. In addition, the individual faces a demand risk, in that a loss would be suffered in the event $E(\theta_2^1) > 0$ and she paid a premium for $p_1 = 1$ to ensure $\varphi_2^1 = 1$, only to discover (later) that $\theta_2 = 0$ and $p_2 = 1$ is not demanded. For a risk averse person, supply risk would elicit a positive premium while a negative premium would be associated with demand risk.

The mainstream literature is summarized by Bishop (1982), who concludes that, in simple formulations of this problem, the net premium is non-negative when $\theta_2^1 = \theta_2^2 = 1$. If demand is uncertain, as well as supply, general statements about the sign of the net premium are elusive. The net premium is called option value (OV). The conventional wisdom is that option price (OP), which represents the future use value of $p_2 = 1$ plus the risk premium (or discount) for $\varphi_2^1 = 1$ is the correct value at $t = 1$ for the state $p_2 = 1$. However, it is appropriate to remind the reader of the reservations expressed by Graham (1981) and Smith (1985 manuscript) and discussed in the text of the present paper.

The "With and Without Principle"

Bishop (this volume) argues that quasi-option value is "nothing special," in the sense that -- if the emergence of new information is predictable -- its conditional value would be attributed to the $p_1 = 1$ alternative in the normal course of applying the venerable "with and without principle" of benefit cost analysis.

The "nothing special" argument seems applicable also to (ordinary) option value. The consequences of risk aversion, where it exists, should ordinarily be incorporated in BCA in the normal course of applying the "with and without principle."

Nevertheless, the concepts of quasi-option value and option value -- even if they are merely specialized application of the "with and without principle" -- serve the useful purpose of drawing attention to certain requirements of ex ante benefit evaluation that might otherwise be overlooked.

Is a More General Analysis of Ex Ante Benefits Under Uncertainty Feasible?

A general ex ante evaluation of benefits under uncertainty requires that risk aversion be considered along with the prospects for emergence of new information about demand, and that the analysis be generalized by dropping the restrictions that p , θ , and φ are binary variables and permitting $p_{t+1} > p_t$ at some finite cost of restoring the preserved state.

However, the special-case problems have been solved because they can be formulated as simple mathematical puzzles soluble with Jensen's inequality (quasi-option value) and simple concavity notions of risk aversion (ordinary option demand). Solution of the general problem, when formulated, will be a more challenging undertaking. Progress is likely to

come in “nibbles,” as less restrictive versions of various special cases are solved.

Again, we are brought back to the total value dilemma. Ex ante total value of benefits is logically coherent and empiri-

cally accessible by CVM. The “taxonomy of value components” approach allows non-CVM methods of estimating ex post benefits of certain uses, but at the cost of persistent internal inconsistency in the taxonomy of value components itself.

Existence Values and Normative Economics

David S. Brookshire, Larry S. Eubanks, and Cindy F. Sorg¹

Abstract.--This paper reviews the various definitions of existence value found in the literature and discusses several issues that are important in clarifying what is meant by existence value. In addition, it is suggested that individuals may express a willingness to pay to preserve nature which may not in all cases be interpreted strictly as an economic benefit.

Resource valuation has evolved dramatically. The methods have improved and the range of resources to be valued and types of values have been expanded. Values have been assigned to wildlife, visibility, health effects and many other resources. The increasing recognition of a larger array of appropriate benefits (such as use, option, existence values) also has greatly expanded the possible applications of benefit-cost analysis.

The question as to what constitutes the appropriate range of types of benefits for use in evaluating decisions involving alternative use of natural environments must be addressed. Now a dollar benefit can be assigned to an array of commodities without the rules of defensibility being well defined. Further, given the ability to assign dollar benefits to natural phenomenon for use in a traditional benefit-cost framework, is the nature of the values in conflict with the normative basis of the benefit-cost framework? It may be given the progress in expanding the versatility of benefit estimation for types of values previously considered unquantifiable. Taken to the extreme, benefit-cost analysis potentially could be utilized to "justify" any proposal.

Consider the question, "What is species X worth?" The economist following disciplinary definitions of value approaches the problem from the perspective of quantifying a use, or option value. In part, the increased range of types of benefits for a larger array of natural phenomenon is the result of the development of the contingent valuation method, which enables monetary quantification of natural assets (Cummings et al. 1986).

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Initially, the CVM conceptual development and empirical applications principally focused on the use or participant benefit values. More recently, researchers have considered other suggested elements of value--option, quasi-option, bequest, preservation, altruistic, vicarious, intrinsic and existence values. Significant effort has been directed toward option value relating to strict definitional interpretations, concern for the proper sign and magnitude, and appropriateness within a benefit-cost framework (Weisbrod 1964, Schmalensee 1972, Graham 1981, Bishop 1982, Smith 1983, Freeman 1984, Smith 1985). A consensus is evolving that option values are appropriate for use and are important in decision-making, especially within a benefit-cost framework.

This paper is concerned with other suggested components. First, a consensus does not exist as to what type of preferences are represented by values associated with existence of natural environments. There appear to be definitional differences and overlaps within the literature. For example, intrinsic, bequest, stewardship, and altruistic values and motives all have been suggested interchangeably or collectively to be part of and/or to represent existence value. For use within a policy framework this issue must be resolved.

Second, existence values do not appear to be bounded relative to other values, such as use value. For example, Greenley et al. (1981) found that existence values, broadly defined, for preserving water quality of the South Platte River in Colorado were 53% of use value. In contrast, Brookshire et al.² found derived existence values for visibility preservation at the Grand Canyon National Park (which were more narrowly defined) were 61:1 relative to user values. Without some better understanding of the possible dominance of existence values, resource managers will have trouble interpreting re-

²Brookshire, D. S., W. D. Schulze and M. D. Thayer, "Unusual Aspects of Valuing a Unique Environmental Asset," Manuscript 1984.

sults of benefit-cost analysis that do or do not include existence values.

Third, given what we later argue existence value to be, all expressions of existence value as willingness to pay measures are not necessarily consistent with the normative basis of benefit-cost analysis. That is, existence values may or may not relate only to the efficiency-based ethic underlying benefit-cost analysis. Thus, inclusions of all monetary representations of existence value in a benefit-cost analysis would be inappropriate.

Sen (1977) distinguishes between sympathy and commitment in asking whether economic models are rich enough to capture behavior that is both maximizing as well as non-maximizing. That is, how is counter-preferential choice, which destroys the traditional assumptions of preference ordering to be viewed? Sympathy characterizes the case in which a concern for others directly affects one's own welfare.

"When a person's sense of well-being is psychologically dependent on someone else's welfare, it is a case of sympathy; other things given, the awareness of the increase in the welfare of the other person then makes this person directly better off." (Sen 1977)

Clearly, behavior based on sympathy will be self-interested and egotistic. Thus, sympathy represents the notion of externalities. In contrast, commitment represents counter-preferential choice.

"One way to define commitment is in terms of a person choosing an act that he believes will yield a lower level of personal welfare to him than an alternative that is also available to him." (Sen 1977)

What is critical to this discussion is that the notion of commitment breaks the identity between personal choice and personal welfare as is traditionally assumed. As noted by Sen (1977), the term "preference" is used to capture this identity. If commitment is related to personally-held ethics, then a wedge is driven between personal choice or behavior and personal welfare. "The basic link between choice behavior and welfare achievements in the traditional models is severed as soon as commitment is admitted as an ingredient of choice," (Sen 1977). Thus commitment represents a case where efficiency is not the underlying criterion in making choices.

Given the framework for normative economics, willingness to pay for the existence of a resource need not have the same normative status as a willingness to pay for a traditional private commodity, if the willingness to pay for a natural environment represents a personal commitment. If so, then elements of existence value are based upon nonefficiency considerations, resulting in problems for inclusion in benefit-cost analysis.

Definitions and Measures of Existence Value

Two quotes from Krutilla (1967) and Krutilla and Fisher (1975) are appropriate to discussion of existence value.

"There are many persons who obtain satisfaction from mere knowledge that part of wilderness North America remains even though they would be appalled by the prospect of being exposed to it" (Krutilla 1967).

and

"Beyond this, a preserved natural environment may be regarded as an open access resource for those who benefit from its existence without necessarily appearing on site to claim their rights or benefits. In this category are:

1. vicarious consumers; those who derive satisfaction simply from knowing that certain rare or remarkable species and environments still exist, and indeed are willing to pay something for their preservation,
2. option demanders; those who value the option of experiencing sometime in the future a particular environment, perhaps for their children and grandchildren, if not for themselves; and,
3. those who may benefit from advances in medicine, agriculture, and so on, made possible by the preservation of genetic information in the more numerous wild species" (Krutilla and Fisher 1975).

Consider this taxonomy as a benchmark. The first type of person identified above, omitting the contradictory vicarious consumer nomenclature, represents the most frequently used statement for existence value. That is, a person is willing to pay for mere knowledge of existence or preservation of a natural environment. No motive other than "knowing" is suggested.

The second category, option demanders, is really two groups. The first represents the standard definition of option value as a willingness to pay to obtain an option to future personal and direct use of the natural resource in question.³ The second group is represented by a willingness to pay for preservation, motivated by the desire that the natural resource be available for use in the future by the individual's children and/or grandchildren. This second type of value is characterized as motivated by "bequest notions" (Krutilla 1967, Randall and Stoll 1983).

The final value in this list is associated with the preservation of genetic information presumably with the opportunity of future use. Krutilla (1967) initially adopted the view that this value followed from a purely scientific viewpoint and, in particular, that there could be a unexpected value of basic research. In contrast, Krutilla and Fisher (1985) refer to values to specific individuals, presumably in the future. Arrow and Fisher (1974) refer to this category of value as a quasi-option value. Specifically, this value is associated with delaying an irreversible decision until the future, when more information may be available.

³A list of the essential literature which contributes to the accepted view of option demand, option value, and option price would include: Weisbrod (1964), Cichetti and Freeman (1971), Schmalensee (1972), Bohm (1975), Bishop (1982), and Smith (1983).

The early suggestions as to what constituted existence value are best represented by notions of knowledge for mere existence of the natural resource. In particular, no other motives, bequest or otherwise, were contained in the definition. Contrast this rather narrow definition with more recent literature.

Fisher and Raucher,⁴ and Randall and Stoll (1983) suggested broadening the Krutilla (1967) definition of existence value. This involves the introduction of motives other than satisfaction associated with mere knowledge of existence.

Table 1 presents information pertaining to empirical studies of existence value. The various structures suggest users and nonusers as master categories as well as an all inclusive category of preservation value. Each study was examined to determine a specific existence value definition and/or the specific CVM question utilized in eliciting existence values in order to illustrate the entwining of values which might be inappropriate.

A wide variety of definitions have been used. Existence value has been defined in terms of desire for participation (Horvath 1974), desires for preservation (Meyer 1974, Schulze et al. 1980, Brookshire et al. 1983), knowledge that a resource exists (Greenley et al. 1980, Walsh et al.,⁵ Desvousges et al.⁶) and non-users.⁷ While all of these are related, there is clearly a lack of consensus as to the exact nature of existence value. Considerations of questionnaire design, vehicles, survey technique and sample size aside, consider the two studies focusing on water quality.^{6,8}

These studies have some commonality in their approaches. Approximately the same categories of water quality were valued (e.g., boatable, fishable, etc.). However, Mitchell and Carson⁸ evaluated the nation's water quality, while Desvousges et al.⁶ evaluated the Monongahela river basin in Pennsylvania. The former study arrived at a \$111 yearly household intrinsic value (e.g., existence value); while the latter arrived at an existence value range, depending upon whether nonusers or users are the focus, of approximately \$42 to \$66 per year. Clearly these results, although internally consistent, are confusing. One is for a specific river basin; the other is for the nation's rivers. Yet, the values are quite similar. Consider the dominance issue mentioned previously whereby

⁴Fisher, A. and R. Raucher, "Intrinsic Benefits of Improved Water Quality: Conceptual and Empirical Perspectives," Draft manuscript, USEPA, Benefits Staff, Office of Policy Analysis, Washington, D. C. (1983).

⁵Walsh, R. G., R. A. Gillman and J. B. Loomis, "Wilderness Resource Economics: Recreation Use and Preservation Values," Written for American Wilderness Alliance, Denver, Colorado (1982).

⁶Desvousges, W. H., V. K. Smith and M. P. McGivney, "A Comparison of Alternative Approaches for Estimating Recreation and Related Benefits of Water Quality Improvements," Report to USEPA, Office of Policy Analysis, Washington, D.C. (1983).

⁷Cronin, F. J., "Valuing Non-market Goods Through Contingent Markets," Report to USEPA by Pacific Northwest Laboratory, U.S. Department of Energy by Battelle Memorial Institute (1982).

⁸Mitchell, R. C. and R. T. Carson, "An Experiment in Determining Willingness to Pay for National Water Quality Improvements," USEPA Draft Report (1981).

visibility values by Brookshire et al.² dominated existence values in comparison to the Greenley et al. (1981) results. Clearly, the choice of value, assuming all other methodological issues aside for each study, will substantively alter the results of a benefit-cost analysis.

The confounding results might arise from the definitional approach for existence value that was utilized, or the nature of the hypothetical market, or the nature of the environmental asset, or the use of a purely hypothetical market where no previous or analogous market even existed, or the underlying motives for the expressed willingness to pay.

Components of Existence Value

Several motivations or forms of consumption have been suggested as elements of existence value including vicarious consumption, bequest, altruistic motives, stewardship, and intrinsic characteristics. These already are incorporated into use and option values. To a large extent, the values fall into the category of sympathy as defined by Sen (1977). That is, these values generally fall into a class of externalities, which in and of itself is not a sufficient condition for inclusion within the existence value category.

Vicarious Consumption

Vicarious consumption is often stated as one motivation for an individual to hold values of existence. Existence value as represented by vicarious consumption suggests that individuals are willing to pay to know that others are using the preserved natural environment. One could analytically characterize such a motive with a model in which utility is interdependent. Such models have been examined frequently in the public finance literature and are often referred to in the context of pareto optimal redistribution (Hochman and Rodgers 1969, Olsen 1969).

Generally there are two ways in which interdependence might be represented: (1) a utility externality or; (2) a goods externality (Daly and Gieritz 1972). A utility externality describes a specification for an individual's utility function as a function of goods and the utility level of some other individual; a goods externality specifies an individual's utility as a function of personal goods consumption and the consumption of a good or goods by another individual. Vicarious consumption can be characterized as an interdependence of the goods externality type. That is, an individual is willing to pay for the preservation of a natural environment because the individual obtains utility from another individual's consumption of a natural environment.

The mere presence of an interdependence in the form of a goods externality does not readily imply that voluntary individual action would fail to efficiently provide preserved

Table 1.--Findings of several empirical studies of existence value.

Authors (Description of Study)	Taxonomy of Values	Existence Value Definition	CVM Question Used to Elicit Existence Value	Mean Bid
Horvath (1973) (Benefits of wildlife in Southeastern U.S.)	Use Value (Consump- tive, Nonconsumptive), Nonuse Value (Con- sumptive, Noncon- sumptive)	Not available	"If you did not participate but wanted to, what amount of daily benefit, expressed in dollars, would you have assigned to fishing, hunting, and wildlife enjoyment?"	Nonparticipation Fishing, ¹ \$28.61 for each day of probable participation; Nonparti- cipation Hunting, \$28.25 for each day of probable participation; Nonparti- cipation Wildlife Enjoy- ment, \$24.52 for each day of probable participation
Meyer (1974) (Salmon in the Fraser, River, British Colum- bia)	Use Value, Option Value, Preservation Value	Preservation value is defined as any value associated with the salmon resource even though the respondent does not expect to use the resource simply because he or she feels the salmon should be preserved	Some people associate a value with environ- mental resources even though they don't expect to "use" them simply because they feel they should be preserved. Please place any value that you associate with preservation below.	Preservation Value, \$223/household/year to maintain the salmon in the Fraser River
Gramlich (1977) (Benefits of attaining a swimmable level of (B) water quality in the Charles River, MA. all other U.S. rivers. Five levels of water quality: A - public water, B - swimming and wildlife, C - some wildlife, D - little wildlife, unpleasant odor, and E - health hazard)	C & D -> B	Not available	"Increase your (family's) taxes \$20 each year and keep clean every river in the U.S. including the Charles River." "Clean up enough for people to swim in and fish and wildlife to live in, but not necessarily good enough for use as a public water supply without further treat- ment."	Inferred Existence Value, all rivers in U.S., \$55.43, all other rivers than Charles, \$25.49; for swimmable water quality, \$/household/ year
Greenley, Walsh and Young (1980) (Water quality improve- ments to enhance recreational enjoy- ment. ² Preserved water quality in the presence of potential irreversible water quality degrada- tion because of mining activity. South Platte River Basin; Denver, Fort Collins, Colo.)	Users (Use benefits, Intrinsic benefits [Indirect, Option, Existence, Bequest]); Nonusers (Intrinsic benefits [Indirect, Option, Existence, Bequest])	"Existence Value is the willingness to pay for the knowledge that a natural environment is preserved."		Non-recreationist: Existence, \$24.98 sales tax, \$6.60 water fee; Bequest, \$16.97 sales tax, \$5.40 water fee; Improved water quality to level A, \$/household/ year

¹Participants averaged 24.9, 14.4 and 118.3 days of participation in fishing, hunting and wildlife enjoyment, respectively.

²Definition of recreational enjoyment was left to each individual.

(Continued) --

Table 1.--continued.

Authors (Description of Study)	Taxonomy of Values	Existence Value Definition	CVM Question Used to Elicit Existence Value	Mean Bid
Schulze et al. (1980) (Grand Canyon and National Parklands in the Southwest)	Use Value (Intrinsic Value), Intrinsic Value	Existence Value is willingness to pay for visibility in Grand Canyon, although the individual may never visit but wishes to preserve a national treasure. Users may also have existence value for clean air quality on days when they don't visit the park.	Not elicited directly	Derived
Mitchell and Carson (1981) (Improvement in levels of water quality [freshwater], boatable, fishable, swimmable; A - swimmable, B - fishable, C - boatable, D - dangerous to human health, U.S. freshwater rivers, lakes and streams)	Use Value (Intrinsic Value), Intrinsic Value	"Intrinsic category, includes a wide array of benefits ranging from indirect benefits to duck hunters of 'clean' water to pleasure gained from knowing that the nation's freshwater bodies have attained a certain quality level" Values expressed by the respondents who do not engage in instream recreation should be almost purely intrinsic.	"What amount on the payment card or any amount in-between, is the most you (your household) would be willing to pay in taxes and higher prices each year to keep the nation's freshwater bodies from falling below the boatable level where they are now. In other words, what is the highest amount you (your household) would be willing to pay for Goal C each year before you would feel you are spending more than it's really worth to you (all members of your household)."	Household, yearly; Intrinsic \$111; \$/house- hold/year
Walsh, Gillman and Loomis (1982) (Maps depicting increases in level of wilderness in Colorado, 1.2 million acres, 2.6 million, 5 million and 10 million, current 1.2 million acres, proposed 5.0 million acres, proposed 10.0 million acres)	Users (Use Value, Option Value, Preservation Value [Existence Value, Bequest Value]); Nonusers (Option Value, Preservation Value [Existence], Bequest)	Existence value is the willingness to pay for the knowledge that natural habitat for plants, fish and wildlife is protected in wilderness areas.	"Assume that the only way to protect wilder- ness areas is for all Colorado households to pay into a special fund to be used exclusively for that purpose. What is the maximum amount of money that you would pay annually to protect wilderness areas?"	1.2 million acres, Existence \$4.87, Bequest \$5.01; 2.6 million acres, Existence \$6.56, Bequest \$6.75; 5 million acres, Existence \$8.86, Bequest \$9.10; 10 million acres, Existence \$11.14, Bequest, \$11.46; \$/household/year, average size of house- hold, 2.7.

(Continued) --

Table 1.--continued.

Authors (Description of Study)	Taxonomy of Values	Existence Value Definition	CVM Question Used to Elicit Existence Value	Mean Bid
Cronin (1982) (Improvements in water quality as described by swimming, boating, fish odor, appearance, ecology, and misc. Five levels of water quality were considered. Potomac River Basin, A - no swimming or fish, strong odor, minimal boating, open sewage; B - no swimming, minimal fishing, boating okay, garbage smell, oil slicks; C - no swimming, safe boating, some sport fish, some occasional odor, slightly murky; D - some swimming, good boating, most all sport fishing, no odor, slightly muddy; E - safe swimming, good boating, larger and better all sport fishing, no odor, fairly clear)	User Value, Nonuser Value	Nonuser is someone who does not use the Potomac, other rivers/ lakes, seashores, or local pools for swimming, boating, fishing, hiking, camping, picnicking, etc. Remember, try to imagine that it is as bad as Condition A and try to estimate the most you would pay each year to get it to the way it is now.	"How much would your household be willing to pay <u>at most</u> in terms of dollars per year to have the water in each of the conditions described on the chart? Let's start with condition B. D -> E." ----- Yearly taxes; assume tax increase would be permanent.	User and Nonuser not separated out.
Desvousges, Smith and McGivney (1983) (Map of river and water quality, 5 levels, no activity, boating, fishing, swimming, drinking; A - safe to drink, B - safe for swimming C - game fish, D - okay for boating E - no activity, Monongahela River)	Use Value (Direct, Indirect [Existence, Aesthetic]), Intrinsic Value, Potential Use (Option Value) (No Use [Bequest, Vicarious Stewardship])	"Existence value is an individual's willingness for the knowledge that a resource exists. That is, an individual--either a user or a nonuser--might be willing to pay something to maintain a high level of water quality at a recreation site in a particular area, even though he will not use it, so that his children may have future use of the site or simply to know that the ecosystem at the site will be maintained."	"What is the most you (and your family) would be willing to pay each year in the form of higher taxes and prices for the goods you buy for keeping the river at level D where it is okay for boating, even if you would <u>never use</u> the river?"	(Indefinite-Implied lifetime); User Existence Value (household) \$65.99; Nonuser Existence Value (household) \$42.12; to keep the quality at level D assume tax and price increase would be permanent \$/household/year

(Continued) --

Table 1.--continued.

Authors (Description of Study)	Taxonomy of Values	Existence Value Definition	CVM Question Used to	Mean Bid
Brookshire, Eubanks, and Randall (1983) (Maintain Grizzly bear and Bighorn sheep habitat in Wyoming under varying levels of supply and demand uncertainty, Wyoming)	Users (Option Price), Nonusers (Existence Value, Option Price)	"Existence value refers to the willingness to pay for the existence or preservation of natural resources." Some individuals may derive satisfaction from knowing that certain species and natural environments exist and, therefore, may be willing to pay for the preserva- tion of such natural resources.		5-year time horizon, bighorn \$7.40, grizzly \$24.00; 15-year time horizon, bighorn \$6.90, grizzly \$15.20; \$/hunters/ 5 or 15 years
Stoll and Johnson (1984) (Total Value measured and components separated, Arkansas National Wildlife Refuge)	On-site Use Value, Off- site Value, (Interper- sonal, Intergenera- tional, Intrinsic)	"Individuals produce existence activities and that the motivation for such production could be attributed to various types of altruism," interpersonal; intergen- erational and Q-altruism (intrinsic).	Suppose that economic pressures and policy changes resulted in a decision to no longer fund programs to maintain the whooping crane population--a decision which would virtually insure the extinction of the whooping crane. Suppose that an independent foundation was set up for purchase and maintenance of refuge land so that species might be preserved in the future. Supporting membership in the foundation would be available for \$__ per year for each person. Future access would be set up so that only those individuals who desire to visit and contribute to the Foundation each year would have the option to use the refuge areas. These people would pay no additional fees for visitation at these refuges. Other individuals who contributed, but did not intend to visit the refuges would still have the satisfaction that they helped preserve the whooping crane. If a supporting membership cost \$__ per year, would you become a member and help insure the contributed existence of the whooping crane?	Per person annually, refuge visitors \$9.33; Texas residents \$1.08; out-of-state residents \$1.24; \$/person/year

environments.⁹ Presumably, an individual's existence value based on this definition has relevance when the marginal utility from an additional dollar paid for preservation exceeds the marginal utility of that dollar spent on the individual's own consumption. If the inequality runs the other way, the individual would prefer the value generated from own goods consumption to preservation of nature for another's consumption. Yet, if this condition holds for an individual's decisionmaking, there would be reason to presume that the individual would voluntarily spend the additional dollar on preservation.¹⁰

Suppose that the other individual, which is the object of an individual's vicarious consumption, is also the object of a third individual's vicarious consumption. This case represents a multi-party externality which has characteristics of a Samuelsonian public good. All individuals vicariously consuming the nature experiences of the same individual benefit when any individual contributes to preservation. In this case, any individual may have a value and may choose to contribute to preservation. However, insufficient preservation would result, because the individual would not be influenced by the external public benefit generated for the other vicarious consumers. Assuming such multi-party vicarious consumption exists, this argument supports the idea that there may be values of economic importance that are not going to be included in market (profit or nonprofit) considerations of choices involving development or preservation of nature.

Furthermore, it is possible that conditions could exist for which a set of multi-party vicarious consumers would agree to involuntary public sector provision of preservation, even though each individual would not voluntarily act to preserve. Each individual might be worse off to contribute an additional dollar to preservation of nature, but would be better off given the multi-party externality if all contributed an additional dollar (Daly and Giertz 1972).

Although vicarious consumption motives can lead to the conclusion that market transactions will not respond to the full social benefit of preserving nature, this is not necessarily representative of existence value. First, characterization of the vicarious consumption of nature is nothing more than a specific case of a good's externality noted in the literature by Daly and Giertz (1972) and others. Second, the statement of existence value as "satisfaction simply from knowing that certain rare or remarkable species and environments still exist" is not the notion of vicarious consumption. Vicarious consumption refers to knowing others consume nature's wonders, not to a value in simply knowing nature's wonders exist and are preserved. Thus vicarious consumption falls into the class of option values. This stems from noting that

⁹This is an important issue for the recommendations made by economists on resource policies, considering the growing interest in the significant economic activities of non-profit environmental organizations.

¹⁰This also suggests that such a discussion can characterize the choices individuals make when they contribute voluntarily to the preservation activities of organizations which are presumably engaged in the provision of a public good (i.e., preserved wildlife and natural environments). Weisbrod (1977) presents a strong argument that non-profit organizations provide public goods rather than private goods.

another's use of nature enters the individual's utility function, and that the other individual cannot be forced to use the preserved natural environment. The willingness to pay for preservation in this case is really willingness to pay to preserve the other individual's option to use of the preserved environment.

Bequest Values

A bequest value occurs when an individual wishes to pay for the preservation of a natural environment so that their children and grandchildren will have the opportunity to use the preserved environment. Many specific motives thus might underlie the act of bequeathing. A bequeathing act based upon a motive held by an individual may be considered another case of vicarious consumption and as such another element of option value. The individual motivated in this way gains utility from vicariously consuming the preserved environment through the expected use made of the environment by the individual's children and grandchildren.

If this is the case, then the altruistic bequest motive (e.g., concern for the welfare of others, as illustrated by the process of bequeathing) can be characterized analytically as an example of intertemporally and interdependent preferences where the externality is of the goods externality type. As such, a bequest motive may or may not result in economic values which are revealed by the market.

On the issue of whether markets will reflect bequest values, note that the bequest motive has been stated by Krutilla and Fisher (1975) explicitly in reference to an individual's children and grandchildren. As the discussion of vicarious consumption points out, for markets to fail, the goods externality must be multi-party. If the bequest value with respect to natural environments reflects concern for one's children and grandchildren, then a multi-party externality is not present. People are known to provide for their children and grandchildren, and it has not been unambiguously demonstrated that in general they fail to satisfy their underlying motives of bequest privately. From the social perspective, if the bequest motive is taken as a multi-party externality, the outcome is not clear, since little work has examined whether nonprofit organizations such as the Nature Conservancy provide an efficient quantity of preservation.

Furthermore, if the underlying motive of bequest is related to an individual's children and grandchildren, it is not likely necessarily to be a cause for the failure of private actions to efficiently preserve nature. A more generalized bequest motive which expresses a concern for the opportunity of future generations to utilize preserved nature could be characterized by a multi-party intertemporal goods externality which is expected to be incompletely internalized by private choices.

Thus bequest value should not be regarded as an element of existence value, because it, like vicarious consumption, can be represented by interdependent preferences. Finally, like

vicarious consumption, a bequest motive has the characteristics of option value, because those who are intended to receive the bequest cannot be forced to utilize the preserved natural bequest.

Altruism

Randall and Stoll (1983) suggest that existence value is altruistically motivated and, therefore, the exhibition of altruism is sufficient for existence value. In particular, they suggest three types of altruism: (1) interpersonal altruism, which is associated with knowing a natural resource is available for use by others; (2) intergenerational altruism, which relates to a value in knowing the resource will be available for future generations; and (3) altruism which comes from the individual knowing that the resource is undisturbed. There are two perspectives from which to view their argument.

First, altruism is simply a concern for the welfare of others. Therefore, Randall and Stoll's (1975) altruism might be included in the previous discussion as intratemporal vicarious consumption or as intertemporal vicarious consumption. Second, use of the term "altruism" may suggest that concern for others may be ethically motivated. If so, then altruism should be treated in a manner to be discussed later. As such, altruism would not appear to be at the root of expressed existence value.

Stewardship

Fisher and Raucher⁴ suggested that stewardship may be a motivational element of existence value. By stewardship, they mean that an individual may be willing to pay for existence because the individual values knowing that ecological diversity is being preserved. Stewardship generally refers to managing another's property, finances, or the affairs of another. As such, it is difficult to think of an individual who is motivated by the feeling of stewardship who only personally values knowing of the preservation of ecological diversity. Thus, the stewardship motive suggests the individual as a "steward" is willing to pay because ecological diversity is part of the affairs of other individuals. Therefore, the relevant economic value is reflected by the preferences of the other person(s).

Another interpretation of stewardship is possible. From an ethical perspective it has been suggested that today's generation should make decisions concerning the use of natural resources as though the present generation does not have ownership of the resources, but is instead the steward of resources that belong to the future. As an explicit ethic concerning how individuals ought to behave, it is appropriate to treat this underlying motive for existence value as we suggest below.

Intrinsic Value

Fisher and Raucher⁴ consider intrinsic benefits (value) as the sum of option values, esthetic existence values, and bequest values. These are interesting concepts for existence

value, because intrinsic means "pertaining to the essential nature of a thing." In other words, intrinsic value would not involve motives for helping, providing or serving others, but involves the nature of the good or resource itself.

Randall and Stoll (1983) suggest intrinsic characteristics as a category of existence value that stems from altruism. That is, there is a willingness to pay from knowing that a natural environment is undisturbed. It is not clear why this form of willingness to pay necessarily requires altruism. Regardless, intrinsic characteristics of a natural resource, whether they are unique or just desirable, are sufficient to generate willingness to pay for knowing a resource exists. Intrinsic characteristics of a resource are what will generate, if any such value exists, an economic rather than an ethical based existence value. However, this interpretation would not include or be a part of option value or bequest value.

This semantic structure offers the dangerous possibility that any apparent willingness to pay that is associated with other definitions of value can be an intrinsic value and attributed to the essential nature of a thing. However, intrinsic seems to suggest a value which is associated with a natural resource in and of itself, regardless of an individually-held value and, therefore, would not be an economic value. However, if the value reflects nothing more than utility or satisfaction which is spawned by a perceived intrinsic attribute of the natural asset, this would seem to correspond to Krutilla's notion of existence value.

Existence Values, Counter-Preferential Choice, and Benefit-Cost Analysis

The discussion to this point leads to the conclusion that the various underlying motives or representations of existence value in the literature are inappropriate measures of an individual willingness to pay for knowing the existence of natural phenomena continues. In fact, they are all consistent with Sen's (1977) concept of sympathy. This section explores further commitment as a motive for such a willingness to pay and which is in the arena of counter-preferential choice.

Specifically, an individual willingness to pay for the existence of natural assets, in part, may be the expression of a commitment to a nonefficiency based ethic. That is, individuals may be willing to pay for a commitment (Sen 1977). If so, this would have implications for the inclusion of all empirical estimates of existence value within normative benefit-cost analysis.

Any estimates of existence value, or more generally any category of benefit, should be based on a definition that is relevant to the underlying normative framework which will be used to make the forthcoming policy recommendation.

The normative basis of the policy recommendations which follow from benefit-cost analysis is composed of three principles (Mishan 1981). The first is that the basis of value is the set of subjective valuations of the individual members of society, and nothing more. Economic value for the society arises from individual preferences which are to be taken as exogenously given. The second principle is that a desirable

policy or allocational change be characterized as a potential Pareto improvement. When analyzing a proposed change from the status quo to a new situation (or allocation), the new situation is said to be a potential Pareto improvement if those who benefit from the change can more than compensate those who are harmed by the change. This situation is regarded as a potential Pareto improvement, because the normative basis for benefit-cost analysis does not require those who benefit to actually compensate those who lose. Combining both principles results in the benefit-cost analysis being constructed as a comparison of the compensating measures of welfare change (variation or surplus) for those who would gain and those who would lose because of the proposed change.¹¹

This second principle refers directly to the notion that individuals reveal their preferences in a consistent and rational manner, thus revealing a preference ordering. All that is required is consistency.

"...no matter whether you are a single minded egotist or a raving altruist or a class conscious militarist, you will appear to be maximizing your own utility in this enchanted world . . ." (Sen 1973).

For that matter, an individual who holds an environmental ethic might be consistent. The relevance to this argument is that existence value might evoke counter-preferential revelations and thus non-efficiency.

A third principle is implicit and also relevant to this inquiry. Benefit-cost analysis is based upon circumstances in which normative economic analysis suggests that market allocation of society's resources will fail to allocate resources efficiently. Normative economics holds to the principle that the proper role for public sector decisionmaking is in attempting to help the market sector attain an efficient allocation of resources. Given the presumption of market failure, normative economics recommends that appropriate public policy be determined by the mix of public sector actions which "pass" the test of benefit-cost analysis. That is, sympathy or externalities are clearly to be examined. Further, benefit-cost analysis can be viewed as representing an efficiency ethic.

Given the normative basis for the benefit-cost analysis, not all values that individuals hold can be appropriately described as an economic value relevant to benefit-cost analysis, and some of these values might even be manifested by the individual as a "willingness to pay."

Suppose, for example, individuals held an ethic, which when involved in a choice problem, is in conflict with an efficiency based ethic? What are the implications for economic analysis, particularly for the notion of existence value? Possibly many such ethics leading to counter-preferential choice exist (Bell 1968) provides one example in an analysis of how the Catholic Church's requirement of meatless Fridays affected commercial fishing.

¹¹Benefit-cost analysis would recommend that all feasible alternative changes in the status quo be compared with the alternative having the greatest excess of benefits over costs being identified as the preferable alternative. In practice, such an extensive comparison of alternatives generally is not attempted.

As another example, consider market boycotts. Some religious leaders have organized boycotts of the products of television sponsors who in their view sponsor unethical television programs. Individual preference might lead to the purchase of boycotted items if it were not regarded as the wrong thing to do. Ethically motivated values and choice behaviors of this sort cannot be appropriately characterized as an argument in individual utility functions. Other examples can be found in the area of environmental ethics.

Regan (1981) argues that a necessary condition for an environmental ethic is that such an ethic "must hold that there are nonhuman beings which have moral standing."¹² A person holding such an environmental ethic would believe that we should consider how nonhuman beings will be affected by our decisionmaking regarding whether or not to take a particular action or adopt a particular policy. From an efficiency perspective this would necessarily involve a counter-preferential choice. This condition, viewed from an economic perspective, suggests that there is a difference between an ethic of the environment, and an ethic for the use of the environment.

An ethic for the use of the environment might be delineated as a management ethic which "would declare that the environment ought to be used so that the quality of human life, including possibly that of future generations ought to be enhanced," (Regan 1981). The management ethic restricts our concern only to the efficient use and interest of human beings. Clearly, benefit-cost analysis which relies on the notion of a potential Pareto improvement represents a framework for expressing a management ethic. Presumably, any one recommending that public policy with respect to wildlife and natural resources ought to be made on the basis of theoretical and applied economic analysis must hold only a management ethic.

The environmental ethic requires that a wedge exists between personal choice and welfare. Suppose an individual holding an environmental ethic has a willingness to pay for wildlife preservation. Such an individual might vicariously consume the wildlife, and/or have a willingness to pay for wildlife preservation as a bequest, but there is something more in the individual's willingness to pay if an environmental ethic is held. Vicarious consumption and bequest motives are associated with the interests of humans and an environmental ethic is concerned with more than simply human interests. An individual may be willing to pay for existence and preservation simply because it is right to try to protect wildlife against human actions which would threaten the existence of the wildlife.

It is in this context that we propose to associate at least one aspect of existence value with an individually held environmental ethic. Value associated with "simply knowing that certain rare or remarkable species and environments exist" is appropriately related to an environmental ethic if the "knowing" relates to something more than knowing, such as in the

¹²Regan also has a second condition which would characterize an environmental ethic. "An environmental ethic must hold that the class of those beings which have moral standing includes but is larger than the class of conscious beings—that is, all conscious beings and some nonconscious beings must be held to have moral standing."

case of issues pertaining to right and wrong. The extent to which these type of existence values are held is an empirical question.

If some portion of existence value stems from a commitment, such as an environmental ethic which views the world from the perspective of right or wrong, then a counter-preferential choice might be made resulting in the environmental ethic being in conflict with the efficiency ethic. Recall, however, that such a situation may not be easily identifiable. A person's choice might coincide with maximization of personal welfare, without this being the reason for the choice. Thus, ethics constrain preference motivated choices, and may actually lead a person to a choice of a less preferred item, because it is regarded by the individual as the right thing to do. This is the point Sen (1977) makes about the notion of commitment. Individuals may behave in counter-preferential ways. If this is the case, it is clearly inappropriate to treat the choice as though it were an income-constrained preferential choice.

Given that existence value is reflected by a willingness to pay for the knowledge of existence and preservation of natural assets, it is, therefore, a value relevant to efficiency, but also may be motivated by a commitment to an environmental ethic. The willingness to pay which is motivated by a commitment stemming from a counter-preferential choice should not be a value relevant to benefit-cost analysis. If there is an economic value in a willingness to pay for existence and preservation, there must be something perceived by an individual which is intrinsic to the natural asset that spawns utility or satisfaction. The intrinsic aspects of an asset and the management ethic are the foundation of economic existence value. For an individual to hold such an efficiency relevant value the individual would have to feel that the willingness to pay was not related to concern for others, present or future, nor was it related to the feeling that it is the right thing to do to help preserve natural assets.

If individuals can be motivated by a personally-held environmental ethic to pay for preservation of wildlife, there is an important implication for benefit-cost analysis. Specifically, a willingness to pay does not always represent an "economic value" as defined within the context of benefit-cost analysis. This is clearly understood when Sen's (1977) discussion of commitment is related to the case at hand. Individual's willingness to pay for preservation being motivated by a commitment to an environmental ethic suggests that a wedge exists between individual behavior and individual choice. The normative basis for benefit-cost analysis relies on the principle that individual choice and preference are the basis for economic value. Treating an ethically motivated willingness to pay for preservation is inconsistent with the normative basis of benefit-cost analysis. The inclusion of ethically motivated values in benefit-cost analysis is inappropriate for the relevant normative economic framework.

Measurement Problems

If existence value is associated with knowing that a resource exists, an appropriate remaining question is, "How should the economic component of existence value be represented in a utility framework?" For discussion, consider a wildlife stock representation.

Miller (1981) and Miller and Menz (1979) suggest that the existence value for a wildlife species may be represented analytically by including the stock of the species in individual utility functions. Their point is that typical treatments of the optimal use of biological populations have considered only the benefits from the flow of services from the wildlife population, and have not considered "the fact that stocks of species are also arguments in individual utility functions, and that preferences for these stocks are not revealed in market-determined prices."¹³ Vousden (1973), Smith (1977) and others have also included stock in utility functions. Plourde (1975) treats the stock of wildlife in utility functions, suggesting that the existence of species is an intergenerational public good.

It is not clear whether the notion of existence value can be meaningfully expressed by including stock in the specification of individual utility functions. The models of Miller (1981) and Miller and Menz (1979) make no distinction between existence value and nonconsumptive user values associated with hiking, backpacking, photography, etc. This certainly would confound analytical efforts. Further, including a stock argument in utility also implies that people are willing to pay greater (but marginally decreasing) amounts for an ever larger stock of wildlife under conventional assumptions. That is "smoothness" over a range of stock sizes is assumed. This may be inappropriate in the existence value context.

The size of a wildlife population may be perceived by individuals as related to its potential for existence, and, as such, a particular stock size above a survival threshold level would lead to the belief that the species was safe. Falling below this threshold, people would perceive a threat to the existence of the species. One might even speculate that individuals perceive the threat of extinction in such a discrete way that the existence value for the species associated with stock sizes greater than zero but less than this threshold would be identical in magnitude. In other words, a-threat-is-a-threat, regardless of the size of the threatened population. Traditional convexity assumptions are inappropriate when discussing existence value. Further problems, however, remain, which even non-convexity recognition would not resolve.

What is the utility value associated with a stock which is zero in size? Is there no satisfaction? This usually is the case with preferences for other goods. However, there is something different about a zero wildlife stock utility argument and a zero

¹³The choice of "fact" in this statement is unfortunate. The authors make little attempt to argue theoretically in support of this fact, nor do they present empirical verification of the "fact." There are several reasons why someone might have a preference for a stock of wildlife, including reasons relating to measurement and motivation ("ethical" or "preference").

for the utility argument corresponding to something like video game consumption. In order to know about the utility associated with a zero for wildlife stock we need to know something about circumstances. For example, suppose individuals believe that the extinction of a species resulted from the economic decisions made by themselves and their contemporaries. In this case, the zero in the utility function corresponding to a wildlife population might well be associated with negative utility.

Suggesting that circumstances may be important relates to observations made by Plourde (1975) and Randall and Stoll (1983), that suggest information plays an important part in the determination of existence values. "It is only when a species becomes endangered that people become aware of their preference for preservation and become willing to pay for it" (Plourde 1975). Also consider a bit of anecdotal empiricism regarding the recent snail darter situation.

"Until its discovery in 1973, its existence demand was zero. Its existence demand rose rapidly as it was accepted as a separate species and listed as endangered, and as knowledge of its existence and its plight spread rapidly among the public" (Randall and Stoll 1983).

These statements may accurately reflect elements of the value people associate with existence of species of wildlife. However, simply including a stock measure in a utility function cannot adequately characterize the concerns of these authors. Surely, including a stock utility term cannot characterize Plourde's (1975) assertion that people become aware of preferences for preservation only when a species' existence is threatened.¹⁴

The obvious question is, "What sorts of things can be legitimately included as an argument in a utility function?" Can we just assume anything as an argument in a utility function?¹⁵ Certainly it is legitimate to write utility as a function of the number of hamburgers, the number of cokes, etc. People are believed to have desires, wants, preferences for such items; but it should be noted that these items have no other special significance apart from the fact that they are desirable.

It is important to ask about the motives that lead people to pay for wildlife stock maintenance. Suppose you ask people

¹⁴This is not meant to overemphasize the importance of these authors' observations for an evaluation of the adequacy of a stock utility argument to express existence value. More importantly, they seem to suggest there are some aspects of existence values for wildlife that will be difficult to account for in the usual types of economic models, and furthermore, that all of existence value may not be totally an economic value in the usual sense. These authors' observations fit very well with treating existence values as being motivated by an individually-held nonefficiency based ethic.

¹⁵Rothenberg (1962) asks what are the alternatives to which preferences are to refer as far as normative economics is concerned. His analysis concludes that individual preferences about welfare criteria should be excluded from consideration as arguments of the individual utility functions that constitute the basis for economic value in the normative framework of benefit-cost analysis.

why they spend money on hamburgers, and also why they spend money on efforts to save the blue whale. Will the nature of the answers to the question be similar, or perhaps dissimilar in an important way? If the answers are similar, it seems legitimate to include measures of both items as arguments in the individual's utility function. If the reasons given are dissimilar in an important way, then we should probably be uncomfortable about including both items in the individual's utility function, or at least about inclusion in the same way.

In summary, expressing existence value as a stock argument in a utility function is incapable of expressing the idea of a value in merely knowing of the continued existence of a wildlife species. Such a representation suggests aspects of existence value which are inappropriate, while at the same time fails to characterize other aspects of relevance. Furthermore, it seems important to describe the motivation for an individual to gain utility from a stock of wildlife. Interest in such a motivation not only suggests that the stock utility representation is ill-conceived, but also that the true character of an existence value is difficult to describe as a simple want or preference.

Conclusions

Many questions remain about the semantic structure known as "existence value." While we argue for a return to the uncluttered world as originally proposed by Krutilla (1967), how then do we measure economic existence value for potential inclusion in a benefit-cost analysis? That is, it is fine to argue that intrinsic characteristics are the root, but how is a willingness to pay preference based measure obtained? Can the contingent valuation methodology accomplish this through a hypothetical market? What about recent arguments that suggest a hypothetical market for existence value would lead to inaccurate values? What about expressions of WTP that are non-efficiency based? Will the CVM allow distinctions amongst alternatives? The list of possible questions is quite long.

Consider initially the issue of efficiency versus ethical confounding. Either all existing empirical measures of existence value to date are efficiency based expressed preferences via a willingness to pay measure, or existing empirical measures are confounded, or they are all willingness to pay measures stemming from non-efficiency ethics. Certainly we can directly inquire as to individuals motives and ethical structures underlying statements of willingness to pay. Designing a series of experiments incorporating these concerns seems possible.

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Intrinsic Values in Benefit Cost Analysis

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Abstract--This paper reviews the literature on intrinsic or nonuse benefits as it has been developed for resource and environmental applications and proposes a consistent set of definitions for *ex ante* use and nonuse values. The conceptual framework demonstrates how the conventional treatment of use, option and existence values is inadequate. Option value, the difference between the option price and expected value of consumer surplus, is shown to arise from comparing two different conceptual frameworks for describing how individuals value resource changes under uncertainty. The *ex ante* or planned expenditure function is defined and used to provide a taxonomy for use and nonuse values when individuals decisions are made under uncertainty. The paper concludes by considering the prospects for measuring nonuse values for natural and environmental resources and the implications for the treatment of nonuse values in conceptual analyses underlying the practices of benefit cost analysis.

Benefit-cost analysis is a set of tools that policymakers can use to judge whether the activities under consideration (e.g., public investments, regulations of private sector actions, etc.) move the economy toward a more efficient allocation of resources. In benefit-cost analysis, positive, aggregate net benefits imply the prospects for an improvement in the status quo; anything else does not.

In the three decades since its acceptance in economics, research in this area has sought to extend the types of benefits that could be measured. The earliest contributions to the field tended to rely on market prices as measures of the dollar benefits associated with public projects (Krutilla 1967). This practice limited the types of goods and services that could be valued to those exchanging on markets. Although public activities provided other outputs, because their valuation was judged to be difficult, these categories of benefits were labeled "intangibles" (Haveman and Weisbrod 1975, Bishop and Cicchetti 1975, Smith 1976).

One of the most important contributions of the research in this area has been the progressive ability to move goods and services from the intangible category (or incapable of valuation) to the measurable. For example, the recreational services provided by projects associated with dams for hydroelectric power and flood control were regarded as intangible until the development of the Travel Cost Model for estimating the demand for outdoor recreation sites. More recently, the hedonic housing market approach has provided a theoretical and, in some cases, empirical basis for valuing site-specific amenities such as air quality (see Bartik and Smith 1987).

One of the "frontiers" in benefit measurement appears to be associated with intrinsic or "non-user" benefits. To date, there has not been an accepted set of definitions or procedures

for measuring these types of benefits. They arise largely from two modifications to the conventional model of consumer behavior. The first, identified originally by Weisbrod (1964), relates to the role of uncertainty for an individual's valuation of certain types of resources. It was argued that, given uncertainty in the use of a resource or its availability in the future, a risk-averse individual might be willing to pay more than his (or her) expected consumer surplus (from that future use) to change the conditions governing the availability of the resource.² Second, individuals may value resources that they do not "use" in terms that would correspond to conventional views of consumption. Krutilla (1967) first proposed this source of benefits, distinguishing bequest motivations from those values identified as "existence values."

These sources of benefits differ in an important respect from early types of intangible benefits. Neither is the result of the process of consumption as it is usually described in economic models. The first arises from motivations that parallel the reasons why individuals purchase insurance or diversify their investments (or activities) in an attempt to reduce their risk.³ In contrast, existence values seem to conflict with the conventional theory of consumer behavior, implying that individuals can gain utility from resources without consumption. Consequently, several economists have

²The use of the term "might" in describing the relationship between an individual's payment and the expected consumer surplus is deliberate. As the past literature has demonstrated, determination of the sign of option value (i.e., the payment or option price less the expected consumer surplus) depends on the assumptions made in characterizing the uncertainty facing the individual and the opportunities available for responding to it.

³Most empirical studies of the magnitude of option value have found it to be as large as the expected consumer surplus (Fisher and Raucher [1984]). By contrast, theoretical attempts to bound option value seem to suggest it should be quite small in relation to user values (Freeman 1984).

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argued that the only legitimate basis for these values is some form of altruism (McConnell 1983, Randall and Stoll 1983).

One purpose of this paper is to argue that neither source of intrinsic benefits must be regarded outside conventional models of consumer behavior. Both are compatible with established models of consumer choice. However, the transition from a consistent conceptual framework for each to their measurement is not clearcut. Consequently, there is ample reason for concern about the use of these concepts to justify a variety of types of policy actions.

Integrating Intrinsic Values Into Consumer Choice Theory

It is important to provide some background on the implicit assumptions underlying conventional models of consumer behavior, especially in relation to existence values, because these have been regarded by some analysts to be at variance with most models of consumer choice. That is, under a narrow interpretation of existence values, the use of a resource is explicitly precluded. Therefore, an individual's valuation of a resource under these circumstances can only arise from some form of altruism. This definition seems to result from a narrow reading of a few key phrases in Krutilla's (1967) original discussion of existence values.

It is more reasonable, and ultimately more productive, to consider what was intended in his discussion. Krutilla (1967) sought to distinguish the observable *in situ* use of an environmental resource from other not easily observable uses for desiring that a particular resource be maintained or enhanced in some respect.

The act of consumption of goods or services in conventional models often assumes the commodities involved are exhausted or "used up" after the individual has purchased and "consumed" them. This perspective is satisfactory for many goods, such as food, but not for others with consumer durables, a notable example of the latter set. However, even within food, purchase and consumption are not always synonymous. Purchase for storage may be an important component of some short-run demand responses (e.g., hoarding of commodities thought to be subject to some future scarcity).

There is a spectrum of goods varying in durability. In each case, there is a relationship between the purchase and time sequence of use. Based on market transactions alone little is known of the nature of instantaneous demands for the services of an automobile, washing machine, or air conditioning unit. Knowing that an anticipated time sequence of uses motivated the initial purchase, it could be assumed, following the analogy to capital theory, that there are conditions when these actions would be completely consistent with those taken in the presence of ideal rental markets for the services involved. Another case that combines several dimensions of the role of time in consumption arises in modeling an individual's decisions for collectible items -- coins, stamps, antiques, etc. There is usually an asset motivation for these decisions arising from the expectation of scarcity-induced price increases. However,

there also may be consumption services in varying degrees provided by the items. The purchase decisions will reflect both of these motivations.

Becker's (1965) early work on the household's allocation of time, and with it the household production framework, has drawn attention to some of these issues. This general line of inquiry is relevant to existence value, because a full evaluation of existence values requires a generic analysis of the way economic models implicitly describe processes of consumption and use of a commodity. In short, to integrate existence values into a model of consumer choice, we must first consider how we use the commodities thought to give rise to existence values. Does the observed action of purchase convey all the information necessary to describe individuals' demand for the services of commodities that might provide existence values?

Consider another example that is more relevant to the class of allocation decisions usually involved in existence value discussions. Walsh et al. (1984) reported the results of a contingent valuation analysis of the wilderness areas in Colorado, eliciting bids from a sample of Colorado residents for differing amounts of land in the wilderness designation. For wilderness recreation, the act of purchase is treated as the trip to the wilderness area. The question relevant to existence values for wilderness areas is whether such trips are the only uses of wilderness. Traditional measures of consumption and use, for example, would exclude the researcher who uses the wilderness (and the wildlife it supports) in his (or her) research.

Moreover, even precluding these technical and scientific uses that are not reflected in the available measures of consumption, there are additional activities, often involving a reasonably large part of some household's leisure time. Individuals join environmental groups, and subscribe to periodicals that describe recreational, sporting, or scientific activities made possible because of the availability of wilderness. These sources of information may be important to some individuals. The growth of environmental and resource related programming on public television is another type of use that is not reflected by the conventional description of purchase and consumption.

These examples are forms of consumption that would not be reflected by the models available to estimate user values.⁴ If existence value is defined to preclude any type of use, then they would be omitted from this classification also. However, an approach that seems more consistent with Krutilla's (1967) objective would be to recognize that for some commodities,

⁴Mendelsohn (1984) has recently questioned the inclusion of some forms of vicarious consumption or secondary use (in his terms) on the grounds that it inevitably leads to higher future use levels and, therefore, is more appropriately captured at that stage. Unfortunately, there is no formal model presented to derive this conclusion. The phenomena of learning-by-doing (or "indirect doing") and consumption decisions are a complex process to model. There are many plausible descriptions of this behavior that would not be consistent with his conclusions. To accept his arguments one must effectively assume that these secondary uses are exclusively desired for information and do not represent utility enhancing acts.

the act of purchasing the good or its services is only one of the ways it can be used. Conventional definitions of user values have treated purchase and use as equivalent. While this is correct for many goods (and circumstances), it may not be for those environmental resources where as existence values may be substantial.

Recognition of a role for these types of consumption in what are termed "existence values" does not preclude the inclusion of altruistic motives as well. Existence value would reflect the types of consumption and indirect (or vicarious) use that are not measured by conventional approaches to describing consumption as well as altruistic behavior. In many respects this approach combines the strategies proposed by McConnell (1983) and Randall and Stoll (1983).

McConnell (1983) followed conventional practice and focused on values in excess of those realized through the "purchase" of the services of the resource.⁵ Thus, if the character or quality of a resource changes, then the Hicksian compensating surplus associated with that change defines the resource value. It includes a change in user and existence values. The former is present because the resource is used by purchasing a good or resource related to the resource, and the latter reflects the change in the value of the resource to the individual in the absence of in situ use. This definition implies that weak complementarity cannot hold.⁶

Our proposal amounts to suggesting that some additional purchases (or allocations of time) may be changed because of a change in a resource. They represent values derived in circumstances where purchases cannot be attributed to the use of the resource or where the actions associated with consumption are not observed. They may be internal to the household (i.e., reallocations of time to reading particular stories in periodicals or viewing specific television programs, etc.). These would be captured in McConnell's (1983) definition, because only one commodity is assigned to use. Implementation of the narrow definition of existence values, as proposed by Randall and Stoll (1983) or Mendelsohn, would require enumeration of all actions associated with consumption and attribution of the purchases of goods or services assumed to be describing uses of the resource. To the extent that some of these consumption choices serve multiple objectives, use measures require a separation of the role of the resource for these activities.

To consider the relationship between the user value and the various components of intrinsic values, it is desirable to evaluate the implications of how a model imposes restrictions on the household's utility function in terms of the relationship

⁵He does express skepticism as to the likely magnitude of these values.

⁶Weak complementarity arises when there is a specific link in an individual's preference function for two commodities. Maler (1974) first proposed this case when one good was private and the other public (or at least not available through markets). It requires that there exists a price for the private good where the quantity demanded of the private good will be zero; and that at that price (and consumption level of the private good) the marginal value of the public good is zero. For discussions of its implications see Freeman (1979) and Bockstael and McConnell (1983).

between a private good, x , and an environmental resource, R . Equation [1] provides the usual formulation.

$$U = U(x, R). \tag{1}$$

There are many choices for the treatment of R in the determination of utility. For example, we could have assumed that R contributed to the production of household service flows or basic commodities (Becker 1965), expressed $U(\cdot)$ in terms of these service flows, and then defined production functions for the service flows. In the two service flow case with x and R as inputs, we need to distinguish whether R can be allocated among the activities or not (we assume x can). The two characterizations would imply a utility function as follows, with $f_i(\cdot)$ representing the household production functions and x_i and R_i the allocations to the i^{th} activity.

$$U = U(f_1(x_1, R_1), f_2(x_2, R_2)) \tag{2}$$

(x and R allocated)

$$U = U(f_1(x_1, R), f_2(x_2, R)) \tag{3}$$

(x allocated)

The distinction between [1] and [2] lies in the fact the R is a "public" input to the household under formulation [3] and not in [2]. Either specification could be treated as providing a rationale for use and existence values, depending on what was assumed about the information available on household choices of x and R and the final service flows associated with $f_1(\cdot)$ and $f_2(\cdot)$.

Further illustration of the implications of the structuring of the role for R in individual preferences arises in the Bockstael-McConnell (1983) analysis of welfare measurement using a household production framework. They noted that it is possible to measure the individual's valuation of a change in the environmental resource (as a non-marketed good) using the demands for one or more marketed goods that are linked to R in a specific manner. These linkages make the individual indifferent to the level of R when the marketed good (or goods) is(are) not purchased. In their analysis, R enters the utility function and not the production functions for household service flows as in equations [2] and [3].⁷ R must be assumed to be weakly complementary to the set of final service flows involving the specific market good as an input. Moreover, this input good must be an essential input to the production of these final service flows.

These conditions effectively "tie" R to the purchase and consumption decisions for a set of marketed goods. Therefore, they eliminate the prospect for existence values. That is, if existence values reflect both enjoyment derived from altruistic and bequest motives and from consumption that is independent of observable acts of use of the resource, then their assumption appears to preclude both. While it might be argued that indirect consumption could be treated as one of

⁷Equivalent conditions could be stated if we assumed that R entered the production functions.

the final service flows, their approach to measuring the individual's valuation maintains that decisions on selections of all the marketed commodities can be observed and are associated with the resource (as a result of the weak complementarity assumption).

Bockstael and McConnell (1983) claim too much for their arguments in suggesting that:

"...it does not matter whether the link between the public good and the produced commodity is through the preference or production function as long as the public good is of no value when the commodity is not produced." (p. 813)

To use their approach to measure the demand for R with data on the purchased goods, we must assume that R is of no value without the purchased commodities. This hypothesis cannot be tested with information on the consumption choices for the purchased goods alone. Although the source for the "no value" outcome whether preferences or production technology is not important to their logic, it is important to gauging the plausibility of the assumptions as a maintained hypothesis.⁸

Randall and Stoll's (1983) formulation of existence values would introduce another function as a separable determinant of utility. This function would involve only the resource, R. This separate contribution could arise because the individual's well being is affected by other economic agents' utility functions at the same time or at different points in time. It might also arise from components of other households' utility functions (i.e., the altruism is a concern for assuring others enjoy the natural environment; comparable psychic income would not be derived from an income transfer).

Although it is easy to characterize the "source" household's preferences for R, any of these assumptions effectively reduces to the specification given in equation [1] in terms of their empirical relevance without information on patterns of usage or specific assumptions on functional structure used to describe utility. Thus, if we assume the household's behavior is best described as a process where each selects good and services to maximize a specified utility function subject to a budget constraint, then McConnell's (1983) use of an expenditure function offers the most direct way to characterize the relationship between user and existence values. By specifying a role for R in the expenditure function that is distinct from that which arises because of the assignment of one or more purchased goods as reflecting the

"use" of the resource, a corresponding role for existence value in the utility function is implied. Moreover, the origins of the existence value can be attributed to any or all of the motives discussed previously.

Let $E(\cdot)$ designate the expenditure function defined formally in equation [4].

$$\begin{aligned} E(P_1, P_2, \dots, P_n, R, \bar{U}) \\ = \min [\sum_i P_i x_i \mid \bar{U} \\ = U(x_1, \dots, x_n, R)] \end{aligned} \quad [4]$$

If one commodity reflects use (e.g., x_1), then the user value derived from any level of the resource (the compensating variation, CV in this definition) is given in equation [5].

$$\begin{aligned} CV = E(\bar{P}_1, P_2, \dots, P_n, R, \bar{U}) \\ - E(P_1, P_2, \dots, P_n, R, \bar{U}) \end{aligned} \quad [5]$$

with \bar{P}_1 - the price at which none of the services of the resource would be demanded. This is simply the area under the Hicksian demand for x_1 between the existing price, P_1 , and the price intercept, \bar{P}_1 .

If there were no resource available (i.e., $R = 0$), then the user value also would be zero. The total value (user and existence) is defined by the difference in expenditures, holding prices constant, but considering the effect of the level of resource available -- zero versus some level R.⁹

$$\begin{aligned} TV = E(P_1, P_2, \dots, P_n, 0, \bar{U}) \\ - E(P_1, P_2, \dots, P_n, R, \bar{U}) \end{aligned} \quad [6]$$

One important aspect of the interpretation of this equation and of existence value, depends on understanding the implications of the link specified between x_1 and R. It implies that there is an additional constraint on the minimization process defined in [4]; x_1 cannot be different from zero unless $R > 0$.¹⁰ Thus, regardless of the price specified for x_1 the level of consumption will be zero if there is no resource. While this seems obvious, it has not been fully appreciated in earlier discussions of the McConnell (1983) framework. It implies, for example, that the expenditures when $R = 0$ will be invariant to the choice of a value for P_1 (for example, $E(P_1, \dots, P_n, 0, \bar{U}) = E(\bar{P}_1, \dots, P_n, 0, \bar{U})$). Consequently, existence value can be defined as the difference in expenditures that would be made at the choke price for x_1 with the environmental resource at zero or a level R as in Equation (7)¹¹ and the sum of use and existence values will correspond to the total value.

⁹This definition exactly parallels McConnell's work, except he focused on changes in the amount of the resource available, rather than its elimination.

¹⁰We could also, without changing the implications of the analysis, assume that R had to exceed some positive threshold for the services to be available. This case might be more appropriate to problems involving endangered species.

¹¹Equation [7] corresponds to Bockstael and McConnell's (1983) equation [16] and, therefore, provides a clear demonstration that their method assumes existence values will be zero.

⁸Their specification is not the same as a technical and observable link between a private and a public good. For example, air quality conditions will be specific to a geographic location. This is observable. In interpreting a distinction discussed in Smith (1981) Bockstael and McConnell (1983) seem to treat this technical link as equivalent to an assumed technological association between a private and public good, as through a household production function. There is an important distinction. The first is observable and, therefore, subject to confirmation. The second is not observable with the present information. Therefore, either assume it is present or use indirect methods to attempt to verify the association. However, these indirect approaches do not exhibit sufficient resolution of the processes involved to permit the testing of the features implied by Bockstael and McConnell's (1983) analysis.

$$EV = E(\bar{P}_1, P_2, \dots, P_n, 0, \bar{U}) \\ - E(\bar{P}_1, P_2, \dots, P_n, R, \bar{U}) \quad [7]$$

If additional purchased commodities are associated with use of the resource, the price arguments in equations [5] and [7] which differ would be increased to include them (McConnell 1983).

The other component of intrinsic value arises from the influence of uncertainty for individual decision-making and valuation. Since all of the preceding analysis has been undertaken with the assumption of consumption decisions given certainty it should not be surprising that the currently proposed benefit taxonomies (Mitchell and Carson¹² or Desvousges et al. 1983) encounter difficulties in consistently integrating the constituent elements within a single behavioral framework. To consider option value one must introduce uncertainty into the process -- either uncertainty as to whether the services will be demanded, uncertainty as to their supply, or both.

The following analysis utilizes the conventional, timeless analysis of option value, beginning with the assumption that the uncertainty relates to an individual's demand for the site's services. Once the option price is paid, supply of the resource is assumed to be available.^{13,14} This approach uses a contingent claims framework with state-dependent preferences to describe the individual's choice problem (Smith 1983). It implies that the model is describing planned actions, contingent on a state of nature being realized.¹²

Nonetheless, all of the arguments concerning the implications of motives in defining a role for resources in the utility function as they have been developed in the certainty case are relevant to this case, and would apply to each of the state-dependent utility functions. Indeed, consumer preferences and those constraints affecting decisions can be represented with an expenditure function for this case as well. However, in this case it is planned expenditures, \bar{E} to realize an expected utility level, and would be defined by equation [8].

$$\bar{E}(P_{11}, P_{12}, P_{21}, P_{22}; \pi_1, 1-\pi_1; R; \bar{E}\bar{U}) \\ = \text{Min} \left[\sum_{i=1}^2 \sum_{j=1}^2 P_{ij} x_{ij} \bar{E}\bar{U} \right] \quad [8] \\ = \pi_1 U_1(x_{11}, x_{12}, R) + (1-\pi_1) U_2(x_{21}, x_{22}, R)$$

¹²Plummer, Mark L. and Richard C. Hartman, "Option Value: A New Approach," *Economic Inquiry*, Vol. 24(July 1986):455-471.

¹³There have been a variety of generalizations to the option value literature, including consideration of: (a) the effects of time sequencing in decisions and the ability to partially resolve some aspect of the uncertainty with time; (b) the prospects of supply and demand uncertainty in a timeless framework; and (c) the use of option price as a payment for a change in the likelihood of uncertain events, but not the elimination of the uncertainty.

¹⁴Bishop, Richard C. "Option Value or Option Price: Principles for Empirical Resource Valuation Under Uncertainty," Department of Agricultural Economics, University of Wisconsin-Madison, April 12, 1984, unpublished paper.

To simplify matters, two commodities and two states of the world are assumed. This implies four contingent commodities, designated with the double subscripts on both the planned consumption, x_{ij} , and prices, P_{ij} (with i designating state and j the commodity). Simmons (1984) proposed similar formulation to provide a measure for a multivariate risk premia with discrete probability distributions.¹⁵ However, his analysis did not recognize the potential value of the framework for benefit analysis under uncertainty.¹⁶ Indeed, this approach provides an alternative to Graham's (1981) willingness to pay locus and allows the definition of valuation concepts that explicitly reflect the implications of the opportunities for individual adjustment to risk. This conclusion follows from the fact that the prices of contingent claims are arguments along with the probabilities of the states of nature of the planned expenditure function. The valuation concepts proposed for risk changes will correspond to Simmons' (1984) proposed measure for a risk premium.¹⁷ Moreover, they can be shown to correspond to the option price when there is no possibility of state dependent payments for the risk change.

To examine the potential value of this framework for benefit analysis under uncertainty and as a comprehensive framework for classifying the sources of individual benefits from public policies that involve changes in risk, consider the conventional definition of the option price. In this framework, it can be described as the maximum payment that would be made in all states for the assured availability of the resource, R . Because this payment is made partly because of the possibility of future use, the definition must allow for that use. Moreover, it is important to recognize that option price implies a specific institutional framework for adjusting to risk. That is, it is a constant payment regardless of the state of the world realized.

As in the case of certainty, to allow for planned use of the resource, a commodity must be designated as representing use. Following conventional practice, assume the two states of nature correspond to the cases where an individual has a demand for use and where he (or she) does not. Thus, there would be no role for the price of the commodity representing use in the no demand state. Following earlier practice, assume it is x_1 . To maintain a constant state dependent payments for access to the resource regardless of the state of the world and the level of use of the resource requires that $P_{11} = 0$. (Note there is no demand for x_1 in state two by assumption; so x_{12}

¹⁵A concept similar to this planned expenditure function was originally introduced by Cook and Graham (1977) for one case -- actuarially fair markets in contingent claims. It can also be treated as generalization of Graham's (1981) willingness to pay locus, allowing for the household to plan different levels of consumption under the various states of the world. Graham's (1981) locus reflects this consumption alternative by allowing differing payments for the same assumed consumption levels in all states.

¹⁶In discussing his proposed risk premium measure, Simmons (1984) draws an analogy to valuation measures in the case of certainty.

¹⁷The most direct correspondence can be seen in his case where risk premia are defined for distributions with differing probabilities but equal mean outcomes.

would not enter the state two utility function.) With these amendments it is possible to define the option price in equation [9].

$$OP = \tilde{E}(\bar{O}, P_{12}, P_{22}; \pi_1, 1-\pi_1; 0; \bar{EU}) \\ - \tilde{E}(\bar{O}, P_{12}, P_{22}; \pi_1, 1-\pi_1; R; \bar{EU}) \quad [9]$$

where \bar{O} designates that $P_{11} = P_{21} = 0$. While there seems to be a parallel between this definition and the definition of the resource value under the case of certainty, there are important differences. First, the expenditure functions are quite different. $E(\cdot)$ is not simply the expected value of the expenditure functions corresponding to each state dependent utility function.¹⁸ Second, this function describes expenditures on contingent claims.

With equation [9] it is possible to illustrate the difficulties posed by the desire for a single framework to include user and intrinsic values. These difficulties arise from the different perspectives associated with the values in the definitions. That is, an ex ante perspective is implied by the definition of option price while an ex post perspective is associated with the conventional definition of the expected consumer surplus. Option value actually involves mixing the two perspectives. That is, in our notation, it requires the difference of the two types of expenditure functions (i.e., option value = $OP - \sum \pi_i CV_i$). This result is illustrated in equation [10], by adapting the definition of CV in equation [5] for the case of two commodities.

$$OU = \tilde{E}(\bar{O}, P_{12}, P_{22}; \pi_1, 1-\pi_1; 0; \bar{EU}) \\ - \tilde{E}(\bar{O}, P_{12}, P_{22}; \pi_1, 1-\pi_1; R; \bar{EU}) \\ - \pi_1 [E_1(\bar{P}_1, P_2, R, \bar{U}) \\ - E_1(P_1, P_2, R, \bar{U})] \quad [10]$$

where $E_1(\cdot)$ corresponds to the conventional expenditure function implied by the utility function in state one. Without a specific relationship between the $\tilde{E}(\cdot)$ and $E_1(\cdot)$ expenditure functions it is difficult to specify the sign of this difference.

The relationship to Simmons' (1984) findings can be readily established by changing the source of uncertainty facing the individual to supply uncertainty. In this case, the individual is certain that the services would be demanded, but is uncertain of their availability. Equation [8] would be restated for this situation as:

$$E^*(P_{11}, P_{12}, P_{21}, P_{22}; \pi_1, 1-\pi_1; R; \bar{EU}) \\ = \text{Min} \left[\sum_{i=1}^2 \sum_{j=1}^2 P_{ij} x_{ij} \right] \bar{EU} \\ = \pi_1 U_1(x_{11}, x_{12}, 0) \\ + (1-\pi_1) U_2(x_{21}, x_{22}, R) \quad [11]$$

¹⁸Smith, V. Kerry, William H. Desvousges and A. Myrick Freeman III, Valuing Changes in Hazardous Waste Risks: A Contingent Valuation Analysis, Vol. I, Draft Interim Report prepared for U.S. Environmental Protection Agency, Vanderbilt University, February 1985.

The option price for an improved probability of availability of R (i.e., $\pi_1' \leq \pi_1$) would maintain that $P_{11} = P_{21} = 0$ (for a state independent payment) as in equation [12].

$$OP^* = E^*(\bar{O}, P_{12}, P_{22}; \pi_1, 1-\pi_1; R; \bar{EU}) \\ - E^*(\bar{O}, P_{12}, P_{22}; \pi_1', 1-\pi_1'; R; \bar{EU}) \quad [12]$$

This is a special case of Simmons' (1984) risk premium and provides an alternative description of the option price concept recently discussed by Freeman.¹⁹

It also is possible to use this framework to define one concept of existence value in ex ante terms. Returning to the original framework of demand uncertainty, user values based on planned consumption, PCV, would be given as:

$$PCV = \tilde{E}(\bar{P}_{11}, P_{12}, P_{22}; \pi_1, 1-\pi_1; R; EU) \\ - \tilde{E}(P_{11}, P_{12}, P_{22}; \pi_1, 1-\pi_1; R; EU) \quad [13]$$

where P_{11} is the price for contingent commodity x_{11} where there is zero demand

Thus ex ante (or planned) existence values PEV would be:

$$PEV = OP - PCV \quad [14]$$

There are both general and specific implications for further taxonomic work in these types of values which follow from this new framework.

1. Concern over the motivations underlying existence values seems misplaced, because it is not clear that it is reflected in any tangible way in the relationships describing how households' decisions are affected by the presence of these motives. In terms of the goal of measuring existence values in either an ex post or an ex ante framework, the source of these values as a result of different types of motives does not seem to have observable implications.
2. A general, all encompassing, conceptual framework for describing values that arise from the use and the existence of the resource must first select a perspective for the analysis. Option value is not relevant to an ex post analysis of welfare changes.
3. To the extent a model that maintains there is uncertainty over the state of individual demand or over the conditions of supply is the most appropriate behavioral framework for analyzing policy decisions, then an ex ante perspective is the appropriate basis for benefit-cost analysis. In this context, the relationship between option price and the expected value of consumer surplus (i.e., the op-

¹⁹Freeman, A. Myrick III, "Supply Uncertainty, Option Price and Option Value in Project Evaluation," Land Economics, Vol. 61(May 1985):176-181.

tion value) is not relevant to the conceptual framework required for evaluating the policy action. Simmons (1984) proposed cost function (i.e., the planned expenditure function) is.

Measuring Intrinsic Values

Part of the motivation for the renewed interest in intrinsic values must be attributed to estimates of their magnitudes in comparison to user values for unique natural environments. For example, Schulze et. al. (1983) found estimates of preservation values for visibility at the Grand Canyon between \$34 and \$52 across four cities in their contingent valuation study.²⁰ When aggregated over all households in the U.S., these estimates implied a value of visibility at the Grand Canyon in the billions of dollars. The portion of this estimate attributed to user values was less than 0.5%. While not as dramatic a contrast in the sources of value, the available estimates of option value from other studies involving less well-known natural environments (many of which would not be considered unique) generally indicate that they are 40-50% of estimated user values (Fisher and Raucher 1984). These findings clearly contrast with Freeman's (1984) empirical bounds for option value in relation to the expected consumer surplus.

This disparity is not surprising. There has been some confusion in the literature on how the various types of benefits considered in an evaluation of decisions involving environmental resources relate to each other. Past efforts at estimating total resource values in the presence of uncertainty have tended to mix perspectives in their approach to valuation of the resource under study. For the most part, these empirical studies have been asking individuals questions that are too vague in comparison to the structure of the conceptual models proposed to explain individual behavior. Moreover, they have elicited responses within frameworks that were not consistent with the theoretical structure that was used to interpret them.

For example, consider the case of eliciting information on option value. The timeless framework for defining option price has been used in most of the contingent valuation studies involving option price bids.²¹ Individuals have been asked valuation questions in two different ways. One approach elicits the option price directly, explaining the potential sources of values of a resource (e.g., the value card in the Desvousges et al. (1983) analysis of option prices for water quality improvements in the Monongahela River) and then asking for the amount expected to be due to use in the future. The second approach asks separately for user and option values (Greenley et al. and Walsh et al. 1984).

²⁰Preservation values are defined in this study in such a way that they have been interpreted as existence values (Randall and Stoll 1983) and as a combination of existence and option values (Schulze et. al. 1983).

²¹Greenley et al. (1981) mention the time of the activities in their descriptions of the user and option value questions; but the time dimension is not directly related to what is being requested of the survey respondents.

Both approaches have limited the information on types of uncertainty, time horizon, mechanism for resolving the uncertainty, opportunities that are available to the individual for adjustment to risk, etc., that have been communicated to the sample respondents. Clearly, one cannot "second-guess" the individual's prospects for using a resource in the future.²² However, what is the "future" to each individual will vary. By adopting a timeless approach to option value, these studies have left the definition of the time horizon to the individual. This may not be inappropriate, if the individual appreciates that the decision must take account of future use over some relevant time horizon. However, to interpret the responses, relating them, for example, to independent estimates of user values, we must know how these responses were formulated. In effect, what time horizon did each respondent consider as relevant to the specified option prices?

Equally important, the ability of individuals to separate components of intrinsic values may be especially difficult. What is attributed to option values may actually reflect existence values, if unobservable future uses are considered in the option price bid but not associated with in situ consumption. This seems to be a likely response, because the questions have tended to define use as in situ use. This conceptual analysis suggests that the contingent valuation questions have tended to ask for planned user values as defined in equation [13] rather than the expected consumer surplus as given in equation [5]. This interpretation follows because the time pattern of use has largely been left undefined. While in some cases information on actual use was elicited (Desvousges et al. 1983), this information did not, as a rule, provide the basis for estimates of user values.

Finally, in the real world individuals must consider many resources in their consumption activities. In many cases the actual "purchases" made of the services of these resources may be limited, especially when considered in relationship to the rest of the households' budgets. Responses to contingent valuation questions on any one of these resources have tended to leave to the individual the matter of forming expectations as to the availability of these other resources.

This discussion of the conceptual frameworks underlying and intrinsic values clearly suggests that these perceptions will influence individuals' valuation responses (i.e., these additional R's would enter both types of expenditure functions).²³ While some contingent valuation experiments have investigated the effects of other public goods on the bids given for specific resources, they have tended to use either general

²²We could, of course, pose as part of the description of the contingent commodity the uncertainty that would characterize an individual's circumstances. This formulation would make the uncertainty a part of the hypothetical conditions presented to the individual.

²³Brookshire et. al. (1985), have often referred to these effects using the Kahneman and Tversky (1982) framework of mental accounts. Namely, that individuals tend to partition their decisionmaking so that choices on particular goods and services only consider a subset of the commodity set. This seems completely analogous to the separability assumptions that under budget decomposability conditions in demand theory.

descriptions of the environmental resources involved or entirely different types of public goods. It is reasonable to expect that the more closely related resources will have larger effects on all dimensions of values, especially for resources that are not unique.

All these issues relate to the use of the contingent valuation approach for benefit measurement. The character of the description of the situation, terms of payment, and the nature of the commodity presented to an individual must be much more complex than it has been if we are to provide a tangible link between the resulting estimates and the theoretical arguments that motivated their development. This added complexity raises genuine questions as to the feasibility of applying the technique.

Nonetheless, estimation of intrinsic values need not be exclusively based on contingent valuation methods. Recent work incorporating risk measures as attributes of housing sites^{24,25} suggests that indirect methods may provide a basis for valuing risk changes acquired through such site selections. These models can be used to estimate the incremental option price-risk relationship when the option price is assumed to be a payment for a change in the odds of some desirable state as in equation [12].²⁶ This approach is consistent with the *ex ante* perspective, and is relevant to the valuation of changes in the conditions of access for some environmental resources. However, it does not provide a basis for estimating *ex ante* existence values. Moreover, to interpret the incremental option price estimates, the analyst must understand how individuals perceive and respond to the risk changes that are assumed to be valued in the model.

Implications

Given the current state of knowledge, appeals to substantial existence or option values in excess of estimated user values in benefits analysis for natural or environmental resources that are not unique must be justified within a carefully designed conceptual framework that recognizes the *ex post ex ante* distinction. The failure of nearly all past empirical studies to appreciate this distinction in the design of their efforts to estimate intrinsic values, as well as problems in their specific interpretations of their results calls for caution in the use of all estimates of option and existence values.

Incorporating intrinsic benefits into routine benefit cost analyses, will require: (1) resolution of the perspective used in evaluating each policy decision in measuring the benefits and

costs that would result from it; (2) consistent and realistic definition of existence values in relationship to that perspective and what is attributed to either actual or planned use; and (3) better understanding of the actual considerations individuals use in valuing resources and how they are communicated in either contingent valuation surveys or in the variables designated to represent the uncertainty and choice factors in indirect benefit estimation methods.

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²⁵Harrison, David Jr. 1983. "Housing Values and the Willingness to Pay for Hazardous Wastes Regulations," Kennedy School, Harvard University, unpublished paper.

²⁶Smith, V. Kerry "Supply Uncertainty, Option Price and Indirect Benefit Estimation," *Land Economics*, Vol. 61(August 1985):303-307.

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Uncertainty and Resource Valuation: Theoretical Principles for Empirical Research

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Abstract--Empirical research on resource values should apply the concept of option price. Option price includes both the expected value of future use and option value, where the latter represents a positive or negative adjustment for the effects of uncertainty on utility. However, additional basic research on the magnitude of option value may have large implications for benefit-cost analysis using market values.

This paper reviews the theoretical literature on option value in order to identify principles that can be applied in empirical research on natural resource values. Suppose a study is being designed to place an economic value on a wildlife resource. The first step would be to focus on current users. These might include both "consumptive users" -- hunters or anglers -- and "nonconsumptive users" -- viewers, photographers, etc. A sample of such users could be surveyed to establish monetary values by applying the travel cost method or contingent valuation. However, both economists and non-economists have asked whether such user values, taken alone, might underestimate the total economic contribution of wildlife and other resources.

One line of reasoning is that people who are not current users and who would not be counted in the user survey, might place a significant value on the option of using the resource in the future. Such options would have value to people, because they are uncertain about future economic parameters, such as preferences, income levels, and resource availability. This "option value" is the focus of this paper.

Weisbrod (1964) published one of the first articles on option value. Bishop (1982) summarized the evolution of the concept. Other recent contributions include Graham (1981), Hartman and Plummer (1987), Smith (1983, 1984), Freeman (1984, 1985) and Chavas et al. (1986). The literature on option value often is very technical and confusing. Researchers need to know what these theoretical contributions imply for valuation studies. The first step is to develop the definitions needed to examine the problem of welfare measurement under uncertainty. Then the theoretical and practical appropriateness of

various welfare measures will be examined, with particular emphasis on the concept of option price.

Option price is defined as either the maximum willingness to pay of consumers to maintain the option of future use or the minimum compensation required to give up the option. For uncertain consumers, option price includes both the expected economic value of future use and option value; the latter is a positive or negative adjustment reflecting the effects of uncertainty on utility. Some attention also will be given to a different concept associated with maintaining future options, the so-called "quasi-option value," as developed by Arrow and Fisher (1974) and Henry (1974).

A second kind of value also may be present among current non-users. There may be people who are not present users and who do not anticipate becoming users in the future, who, nevertheless, would place a value on the continued existence of a resource. Such existence values are not treated here (Krutilla 1967, Krutilla and Fisher 1975, Randall and Stoll 1983, McConnell 1983, Fisher and Raucher 1984, and Boyle and Bishop 1987).

Appropriate Measures in Cost-Benefit Analysis

The easiest way to define the problem to be confronted here is to develop in detail the hypothetical example posed earlier. Suppose that a study is being conducted to value a wildlife resource (e.g., an elk herd within a given area of national forest). The context might be a proposed mining project that would eliminate habitat necessary to the elk herd's survival. Also, suppose that, based on a user survey, contingent valuation and/or a travel cost model are used to estimate the present period consumer surplus of users. After expanding the study results to the population of present users, the estimated

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annual value of the elk herd to all present users is determined. Assume for the sake of discussion that this estimate is accurate.

Next, suppose that Mr. Citizen steps forward to argue that his value for the elk herd was overlooked. He was not a user in the present period and was not counted in the user survey, but indicates that he may become an elk viewer in the future and would be willing to pay \$100 right now to be certain that this elk herd will be available in the future. What should be done with this \$100 value? Should it be added to present benefits, to future benefits, or should it be ignored?

Building more detail into this scenario, let's ask Citizen to provide more information. Why would he pay \$100 now? Suppose that he is uncertain about whether he will actually make an elk viewing trip in the future. If he decides to go, he will get \$175 in consumer surplus. If he decides not to go, then his future consumer surplus from the elk herd will be zero. The decision about whether or not to make the trip depends on whether he can persuade a specific friend to go. Right now, he figures that the chances are about even that his friend will agree to accompany him. To keep it simple, suppose that the friend is a marginal elk viewer in the sense that she will not derive any consumer surplus from elk viewing whether she agrees to make the trip or not.

Citizen's bid of \$100 is his "option price." It represents his maximum willingness to pay in the present for the option of viewing elk in the future. It is what is termed an "ex ante value." Ex ante values are payable in the present for possible use in the future. They are determined while consumers may be uncertain about future preferences, income levels, resource availability, or other economic parameters. Citizen's "conditional consumer surplus" values of \$175 if he goes elk viewing in the future and zero if he does not are "ex post values." They are determined after the uncertainty has been resolved and are, at present, conditional on the state of the world.

Ex ante values (option prices) and ex post values (conditional consumer surpluses) are alternative welfare measures. Citizen would be willing to pay \$100 now for the option of viewing elk in the future or he would be willing to sign a contract to pay either \$175 or zero in the future conditional on his decision to take a trip or not to take a trip. Given the even odds of his taking a trip, a third alternative welfare measure, the "expected value of consumer surplus" is $0.5(\$175) + 0.5(0) = \87.50 .

The third welfare measure, expected consumer surplus, has played a central role in the option value debate. Because option price and the expected value of consumer surplus are alternative monetary expressions of the same possible levels of utility, it would make no sense to add them. Citizen's value of future elk viewing opportunities is not \$187.50 (option price plus expected consumer surplus). To commit this error would be to fall into a double-counting trap first recognized by Long (1967). The monetary measure of value is either \$100, if the ex ante measure is the correct welfare measure or \$87.50 if the expected value of the ex post measures is chosen. Stated differently, Citizen would not both pay \$100 now and sign the

contract for ex post payments of \$175 or zero. The issue becomes one of identifying which measure is correct.

Option price and expected consumer surplus need not be equal. The difference between option price and expected consumer surplus ($\$100 - \$87.50 = \$12.50$) is "option value" which can be interpreted as an ex ante allowance for the uncertainty that Citizen has about whether the trip will occur. Furthermore, while this paper's discussion has been cast in terms of consumer surplus, all the definitions are easily translated into "exact" welfare measures (Schmalensee 1972).

To reiterate, three distinct potential measures of the value Citizen places on elk viewing opportunities have been identified: (1) option price; (2) conditional, ex post consumer surplus values, one for each possible future state of the world; and (3) the mathematical expectation of the ex post consumer surplus values. The problem is to decide which measure to use in cost-benefit analysis. To develop a proposed solution to this problem, it will be necessary to inquire more deeply into the welfare theoretical basis of cost-benefit analysis.

Cost-Benefit Analysis Under Uncertainty

The welfare theoretical justification for comparing benefits and costs is the potential Pareto improvement criterion. The cost-benefit analyst is asking whether the "gainers" from a proposed project or policy could compensate the "losers." This criterion is termed the "compensation test." Note that the compensation test makes no presumption about whether compensation is actually paid. It is often noted that the analyst should develop information on the "distributional implications" of the decision; but whether compensation of losers is actually accomplished is left to non-economists.

Current practice is to conduct this exercise as if gainers and losers are operating under certainty. Early writers (Eckstein 1965) did advocate adjustments in the discount rate to reflect the greater relative uncertainty of some projects. This has continued to be a controversial suggestion, and more recent writers (Arrow and Lind 1970, Graham 1981, Chavas et al. 1986) have tended to strengthen the theoretical arguments for the riskless rate of discount. Thus, the theory of cost-benefit analysis under uncertainty tends to focus more directly on the compensation test itself (Ulph 1982). How should the compensation test be applied when gainers and losers are uncertain?

One possibility is termed the "ex post compensation test." According to this criterion, a project or policy is deemed economically feasible if the gainers can fully compensate the losers in all states of the world. That is to say, the analyst would estimate the benefits and costs in each and every state of the world, and judge the project or policy as having passed the ex post compensation test only if net benefits are positive in all possible future states of the world.

Another possibility is the "ex ante compensation test." Ex ante gainers are those with higher expected values of utility, while the opposite would hold for ex ante losers. The ex ante

compensation test examines whether ex ante gainers can compensate ex ante losers. Stated differently, the ex ante compensation test asks whether the aggregated option prices of ex ante gainers in terms of willingness to pay exceeds the option prices of ex ante losers in terms of willingness to accept compensation.

The third possibility is termed the “expected compensation test.” Letting ex post willingness to pay be measured in a positive direction and ex post compensation demanded be measured as negative, gainers under this test will have positive expected values of ex post economic surplus while losers will have negative expected values. A project or policy passes the expected compensation test if the sum of these expected values across all gainers and losers is positive. This test boils down to requiring that “on the average” ex post gainers can compensate ex post losers.

This list of three possible compensation tests does not exhaust all possibilities. In fact, in the next section, a fourth possible measure of value based on the “fair bet point” is considered. Here, it is argued that the ex ante compensation test is preferred among the three possibilities just listed.

The ex post test has practical shortcomings. It is likely to be difficult to evaluate benefits and costs in all conceivable future states of the world. However, for many projects and policies it will not be necessary to do so. All that is required to reject a proposal is to find one plausible future scenario with negative net benefits. Therefore, probably only a few proposals would have to be considered in detail. Practical applications of the ex post compensation test could involve acceptance of proposals only if they have positive net benefits over a wide range of plausible future scenarios.

Objections to the ex post compensation test are at least as much conceptual as practical and can be stated as a rhetorical question. “Would society want to reject all projects for which there exists one or more plausible future scenarios with negative net benefits?” Such a rigorous criterion could introduce the same sort of paralysis that would exist under certainty if the full Pareto criterion were applied. Under the full Pareto criterion, proposals would be adopted only if they would make at least one member of society better off and leave no one worse off. Such a criterion would mean rejection of most, if not all, proposed policies and projects. The compensation test was developed to recognize explicitly that society may wish to accept proposals even though some people may be left worse off. Thus, the compensation test, with an explicit caveat that distributional effects also should be considered, has become the norm.

Similarly, society may wish to proceed with proposals that entail a risk of negative net benefits in some plausible future states of the world. Both the ex ante test and the expected compensation test are consistent with this less conservative view.

In choosing between the ex ante and expected compensation test, the former seems more appropriate. The ex ante test reflects tastes and other economic parameters at levels that exist when the decision is being made (Ulph 1982). The

expected compensation test neglects the fact that proposals not only provide goods and services, but also affect people through the uncertainty they feel. Ex ante measures (i.e., option prices), include adjustments for this uncertainty. This adjustment is option value.

Therefore, out of the three welfare criteria discussed so far, the ex ante compensation test is preferred. Its implementation in valuation research would involve the measurement of option prices. The caution regarding the examination of distributional effects still holds after uncertainty has been introduced. A second caution is also appropriate. Proposals that pass the ex ante compensation test and are judged to have acceptable distributional implications may still be rejected if, under some plausible future scenarios, unacceptably large negative ex post net benefits could occur. As with distributional effects, the judgment of unacceptable risks would be left to the social decision maker. However, it would be incumbent on the cost-benefit analyst to examine not only ex ante benefits and costs but also worst case scenarios. This approach to uncertainty goes back to the writings of Ciriacy-Wantrup (1952, 1985) and has been more recently advocated in the context of endangered species policy by Bishop (1978).

Theoretical Arguments for Ex Post Measures

Some theoreticians are not so willing to reject ex post measures. An important dimension of uncertainty and welfare has been neglected. Once uncertainty is introduced, there is the additional issue of the allocation of risks. A potential problem with basing cost-benefit analysis on option prices is that, by constraining consumers to the same payment regardless of the state of the world, opportunities to reallocate risks across states in ways that improve welfare are overlooked.

To see what is involved, it will be useful to introduce the willingness-to-pay locus (Graham 1981). Recall that Mr. Citizen is indifferent between paying the option price (\$100) with certainty and signing a contract to pay his consumer surplus (zero or \$175), conditional on the state of the world in the future. Other contingent ex post payments may be equally satisfactory in the sense that they yield equal expected utility. For example, Citizen might be equally happy to sign a contract to pay \$25, even if he decides not to make the elk viewing trip, provided that he would be required to pay only \$160 if he does make the trip. Other ex post payment combinations may be equally palatable. The locus of all payment combinations yielding the same expected value of utility as option price (including the conditional consumer surpluses) constitute the willingness to pay locus as illustrated in figure 1.

The vertical axis in figure 1 shows the payments that will be made if the elk viewing trip is demanded, while the horizontal axis expresses payments if the trip is not demanded. Point A is the option price, because it involves the same payment (\$100) whether the trip is demanded or not. Point B represents the conditional consumer surplus values, a contract for ex post payments of \$175 or zero depending on whether a trip is

demanded. Point C represents ex post payments of \$160 or \$25, depending on whether a trip is demanded. Connecting all points which are equally palatable to Citizen in terms of the expected value of utility forms Citizen's willingness-to-pay locus.

This graph can be used to review the relationship between option price and consumer surplus. The expected value of consumer surplus is shown as point D. In this case, option price is the larger of the two making option value (OE minus OD) positive. However, a different willingness-to-pay locus could yield the opposite sign for option value.

Furthermore, figure 1 illustrates the fact that option price and conditional consumer surpluses are only special cases of an infinite number of state dependent payments that Citizen would find equally acceptable. So far, we have only discussed three points on the locus--option price, the consumer surplus point (0, \$175), and the point (\$25, \$160)--as well as one other point, (\$87.50), the expected value of consumer surplus, which in this case lies inside the locus. Another point on the locus is potentially relevant for welfare evaluation, Graham's (1981) "fair bet point."

Suppose that it is desirable to maximize the expected value of ex post payments, \bar{P} . Let P^i ($i = 1, 2$) be the state dependent payments where, in state 1, the trip is demanded, and in state 2 it is not. Let the probabilities of the respective states be π^i ($i = 1, 2$). In the example, $\pi^1 = \pi^2 = 0.5$; but, to be slightly more general, allow π^i to vary with $\pi^1 + \pi^2 = 1$. Thus, the assumed objective is to maximize

$$\bar{P} = \pi^1 P^1 + \pi^2 P^2 \quad [1]$$

subject to the willingness-to-pay locus. The latter can be defined with the help of state dependent indirect utility functions $U^i(Y)$ ($i = 1, 2$) where \bar{Y} equals income which is assumed to be Y regardless of the state of the world. All other variables in the indirect utility functions are constant and have

been suppressed for notational convenience. $U^i(Y)$ are the state dependent utility functions when elk viewing trips are available. Let \bar{U} = the level of utility attainable if no elk viewing trips are possible because of mining development, which is assumed constant regardless of the state of the world. Then the willingness to pay locus is all combinations of P_1 and P_2 such that

$$\pi^1 U^1(\bar{Y} - P^1) + \pi^2 U^2(\bar{Y} - P^2) = \bar{U} \quad [2]$$

Note in passing that consumer surplus P_S^i is defined by

$$U^i(\bar{Y} - P_S^i) = \bar{U} \quad (i = 1, 2) \quad [3]$$

where, by assumption, $P_S^2 = 0$ for Mr. Citizen. Also, option price is defined by $P_O^1 = P_O^2 = P_O$ such that $\pi^1 U^1(\bar{Y} - P_O) + \pi^2 U^2(\bar{Y} - P_O) = \bar{U}$. Maximizing (1) subject to (2) and rearranging and simplifying the first order conditions indicates that at the maximum (assuming concavity of the $U^i(T)$),

$$U_Y^1(\bar{Y} - P^1) = U_Y^2(\bar{Y} - P^2) \quad [4]$$

where U_Y^i is the partial derivative of U^i with respect to income. Thus, the point that maximizes the expected value of ex post payments, denoted by (P_f^1, P_f^2) , is that point on the willingness-to-pay locus where the marginal utilities of income in the two states are equal. This is the "fair bet point" (Graham 1981). Graphically, this point can be identified by first taking the total differential of [2] and rearranging to obtain:

$$\frac{dP^1}{dP^2} = - \frac{\pi^2 U^2(\bar{Y} - P^2)}{\pi^1 U^1(\bar{Y} - P^1)} \quad [5]$$

which is the slope of the willingness-to-pay locus. This can be interpreted as the marginal rate of substitution between income in the two states. At (P_f^1, P_f^2) , where conditional marginal utility levels are equal, the utility terms cancel leaving

$$\frac{dP^1}{dP^2} = - \frac{\pi^2}{\pi^1} \quad [6]$$

Thus, at the fair bet point, the slope of the willingness-to-pay locus is equal to the negative of the inverse of the probabilities. This is shown as point of tangency G in figure 1 where the line tangent to the locus has a slope equal to the probability ratio on the right side of [6].

It follows from the definition of the fair bet point that the expected value of ex post fair bet payments is greater than or equal to the expected value of consumer surplus as well as option price, a conclusion with an intuitive interpretation. Suppose Mr. Citizen can obtain the option of taking the elk viewing trip by signing a contract for any combination of payments along the willingness-to-pay locus. The fair bet point is of special significance because it allows him to equalize the conditional marginal utilities of income across states. Application of this equimarginal principle would allow him to reallocate income between states by making state dependent payments in an optimal way. Thus, he is willing to pay more in

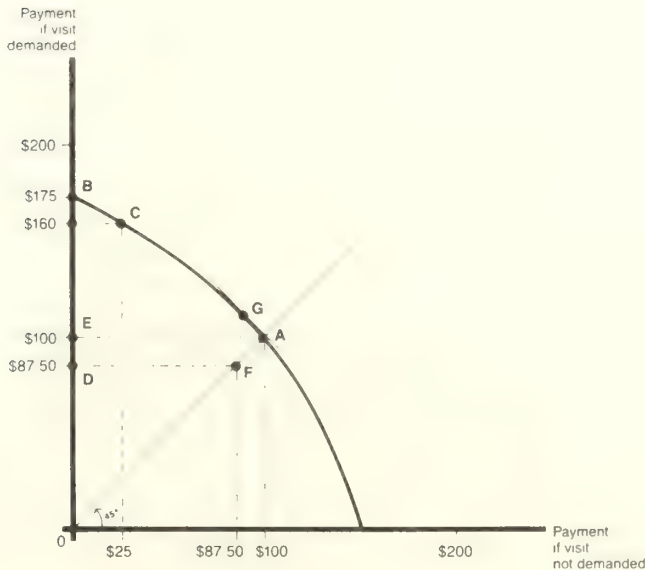


Figure 1.--Mr. Citizen's willingness to pay locus.

expected value terms to sign a contract for the ex post fair bet payments than for any other combination of payments, including the option price. At the fair bet point, Citizen achieves an optimal allocation of risk across states.

The fair bet point takes on even more significance in the context of competitive contingent claims markets. In such a set of markets, assuming (1) zero transactions costs, (2) large numbers of people with different state dependent utility functions who agree on the probabilities, and (3) smooth concave willingness-to-pay loci for everyone, consumers would exchange contingent commitments to pay given amounts until each arrives at a fair bet point on one of his or her willingness-to-pay loci. Thus, because probabilities are agreed upon by all, the marginal rates of substitution between income levels in alternative states will be equalized across consumers. (Note that each consumer will have a series of loci, one for each expected utility level.) In this way, a Pareto optimal allocation of risk among consumers would be established. It also turns out that the sum total of the willingness to pay of all consumers would be a constant across states, although it would not be clear which consumer would pay which amount until the state of the world became known. This point is worth considering, because it means that with perfect contingent claims markets it would be possible to know with certainty ex ante the aggregate willingness to pay of all citizens and this aggregate willingness to pay would be the same regardless of the state of the world that finally occurs. It also would be greater than or equal to aggregate option price and aggregate expected consumer surplus. These points are proven by Graham (1981).

These arguments mean that government might improve social welfare not only by altering the allocation of resources, but also by improving the allocation of risk. Perhaps this is already occurring to the extent that government fosters and regulates futures markets and private insurance and establishes public insurance programs for hazards such as flooding and crop failure. However, there appears to be little attention to seeking out improved risk sharing arrangements in the design of user fees for public projects. Perhaps research will identify new ideas for increasing the benefits and reducing the costs of public projects and policies through state dependent payment and compensation schemes.

Meanwhile, this framework would appear to be of limited relevance to applied research on resource and environmental values. For each gainer and loser to reach a fair bet point, either complete private contingent claims markets would have to be established or government would have to develop a repayment scheme that would imitate the market equilibrium. Mendelsohn and Strang (1984) argue that moral hazard, adverse selection, and the probable complexity of risks faced by real world consumers and producers make the evolution of such a set of markets unlikely. Furthermore, they argue, these same factors will form impediments to governmental implementation of payment schemes to attain fair bet points. Graham (1981) concluded that, "... option price may be regarded as a 'second best' measure of benefit appropriate to situations in

which (1) actual financing involves sure collections from individuals, and (2) secondary contingent claims markets are not available."

As a practical compromise, the ex ante compensation test continues to be the appropriate foundation for applied cost-benefit analysis under uncertainty. In the example involving Citizen's elk viewing, option price is the best practical welfare measure. Additional research may identify ways to improve the allocation of risk among economic agents, but existing theoretical work in this area appears to be of limited relevance to applied research on resource and environmental values.

Quasi-Option Value

There is a second concept which is sometimes referred to as option value (Henry 1974; Hanemann 1983; Fisher and Hanemann 1986). However, this "second option value" is a very different concept from the one discussed so far. Arrow and Fisher (1974) and Conrad (1980) use the term "quasi-option value." This discussion of quasi-option value draws heavily on Hanemann's (1983) paper and adaptations in Fisher and Hanemann (1986).

Assume two periods, $t = 1, 2$. In keeping with our elk watching example, assume that the mine can be initiated now ($t = 1$), in the future ($t = 2$), or not at all. Following Hanemann's (1983) exposition, let d_1 = the amount of mining development in the first period, $0 \leq d_1 \leq 1$, where unity here represents full development. Similarly, d_2 is the amount of mining development in period 2. Full development is an upper bound (i.e., $d_1 + d_2 \leq 1$), and we will assume that development is irreversible ($d_2 \geq 0$). Associated with development is some level of net benefits, B . For convenience, we can use the additive form:

$$B = B_1 + B_2,$$

where B_1 and B_2 are present and future net benefits, respectively. More complex forms are, according to Hanemann (1983), equally adaptable to the analysis that follows.

The function B takes into account all the benefits and costs of the decision. Thus, we can say that:

$$B_1(d_1) = B_{1d}(d_1) + B_{1p}(d_1)$$

where $B_{1d}(d_1)$ is the first period mining benefits, net of investment and operating costs, as a function of the size of the mining project and B_{1p} is first period elk viewing benefits, net of any costs for elk viewing facilities (e.g., parking lots, trails, etc.). These magnitudes are assumed to be known with certainty. Second period net benefits depend on the total level of development and the increment of development in the second period. Also assume that second period benefits depend on some random variable, θ , which has a known distribution. That is:

$$\begin{aligned} B_2(d_1 + d_2, d_2; \theta) \\ = B_{2d}(d_1 + d_2, d_2; \theta) \\ + B_{2p}(d_1 + d_2, d_2; \theta). \end{aligned}$$

To illustrate quasi-option value, the traditional assumption (Arrow and Fisher 1974) is made that d_1 and d_2 are either 0 or 1. That is, partial development is not possible. Either the full mining project is implemented or it is not. Also, it will be assumed that, while θ is uncertain now, it will be known with certainty at the beginning of period 2. Suppose, though, that a mistaken decision maker fails to include in his or her calculations the fact that full information will be available before d_2 must be determined. Given the mistaken decision maker's assumption (i.e., no new information), the objective function can be stated, following Hanemann (1983) (see also Fisher and Hanemann 1986) as a two-stage decision problem of maximizing

$$\begin{aligned} U^*(d_1) &= B_1(d_1) \\ &+ \max_{d_2} [E\{B_2(d_1 + d_2, d_2; \theta)\}] \\ d_1 + d_2 &\leq 1 \\ 0 &\leq d_2 \end{aligned}$$

In contrast, a correct decision maker would include the forthcoming information in his or her decision calculus. The optimal value of d_2 can be determined with perfect information once $t = 2$ arrives and the correct decision maker's two-stage problem is to maximize

$$\begin{aligned} \hat{U}(d_1) &= B_1(d_1) \\ &+ E\{\max_{d_2} [B_2(d_1 + d_2, d_2; \theta)]\} \\ d_1 + d_2 &\leq 1 \\ 0 &\leq d_2 \end{aligned}$$

Both V^* and \hat{U} measure the expected value of total benefits over both periods as functions of d_1 . The only difference is in the effects of the information assumption.

With the constraint that $d_t = (0, 1)$ for $t = 1, 2$, we can find the solution under each information assumption by comparing two values. For the mistaken decision maker,

$$\begin{aligned} U^*(0) &= B_1(0) + \max [E\{B_2(0, 0; \theta)\}, B_2(1, 1; \theta)] \\ U^*(1) &= B_1 + E\{B_2(1, 0; \theta)\} \end{aligned}$$

The decision would be based on whichever is larger. Thus, the solution is:

$$d_1^* = \begin{cases} 0 & \text{if } U^*(0) \leq U^*(1) \\ 1 & \text{otherwise} \end{cases}$$

For the correct decision maker, the comparison would be between:

$$\begin{aligned} \hat{U}(0) &= B_1(0) + E\{\max [B_2(0, 0; \theta), B_2(1, 1; \theta)]\} \\ \hat{U}(1) &= B_1(1) + E\{B_2(1, 0; \theta)\} \end{aligned}$$

Thus,

$$\hat{d}_1 = \begin{cases} 0 & \text{if } \hat{U}(0) \leq \hat{U}(1) \\ 1 & \text{otherwise} \end{cases}$$

Note that because of irreversibility,

$$\hat{V}(1) = V^*(1).$$

If preservation is chosen by the correct decision maker, development can always take place in the second period if the information warrants it. New information prior to the beginning of the second period could not possibly reduce the expected value compared to the case of no new information and might lead to a higher expected value. In mathematical terms:

$$\begin{aligned} E\{\max [B_2(0, 0; \theta), B_2(1, 1; \theta)]\} \\ \leq \max [E\{B_2(0, 0; \theta)\}, B_2(1, 1; \theta)] \end{aligned}$$

This, in turn, implies that:

$$\hat{U}(0) \geq U^*(0).$$

Thus, the correct decision maker can achieve an expected value that is just as large or larger than the expected value attainable by the mistaken decision maker. It is also intuitive that the incentives not to develop (i.e., setting $\hat{d}_1 = 0$) are stronger for the correct decision maker. Preservation ($\hat{d}_1 = 0$) leaves her or him flexible to adapt to whatever θ turns out to be while $d_1 = 1$ is irreversible and commits her or him to the mine regardless of θ . The prospect of learning θ with certainty prior to deciding on d_2 is an incentive to keep the option open. Stated mathematically, the mistaken decision maker preserves if

$$V^*(0) - V^*(1) > 0$$

while the correct decision maker preserves if

$$\hat{V}(0) - \hat{V}(1) > 0$$

and

$$\hat{U}(0) - \hat{U}(1) \geq U^*(0) - U^*(1).$$

The correct decision maker has a larger incentive to preserve.

In this context, quasi-option value can be defined as a tax on the mistaken decision maker, levied if development is chosen in the first period, which is sufficient to make him or her behave like the correct decision maker. Letting τ represent this tax, it would be defined by

$$\hat{U}(0) - \hat{U}(1) = U^*(0) - [U^*(1) - \tau]$$

or, after rearranging and canceling equal terms

$$\tau = \hat{U}(0) - U^*(0).$$

The relationship between quasi-option value and the value of information can be seen here. Based on the assumption of no new information, the mistaken decision maker was only able to generate an expected value for preservation of $V^*(0)$ while the correct decision maker, recognizing that new information is in the offing, can attain an expected value for preservation which is just as high or higher [$\hat{U}(0)$]. The difference is quasi-option value. That is, another way to define quasi-option value is as the expected value of perfect information conditional on choosing preservation in the present (Hanemann 1983).

Though brief and somewhat stylized, this example illustrates two conclusions about quasi-option value. First, the framework of analysis from which it is drawn, with its explicit attention to irreversibility and changing information, may well contain the most important ideas for improving project evaluation in the recent literature. Cost-benefit analysts have implicitly assumed that all decisions are equally irreversible when, in fact, this is not the case. The current state of the art in applied cost-benefit studies makes the analysts into mistaken decision makers. The framework drawn upon to devise quasi-option value is potentially very rich in insights about correct project evaluation procedures, optimal timing of investments, and optimal levels of information gathering (Miller and Lad 1984). Further attention to these insights could revolutionize cost-benefit analysis.

The second conclusion is that the concept of quasi-option value itself is nearly useless for applied research on individual resource values. For example, it would make no sense to ask people in questionnaires what their quasi-option values are, even assuming one could word an understandable question to do so. Only respondents who are behaving like mistaken decision makers will have such values. Stating the same point somewhat differently, if the government has enough information to set τ , why doesn't it just give people the information?

Beginning from the other direction and asking people how large their quasi-option values would be if they were mistaken would not be helpful either. Results would be arbitrary in the sense that quasi-option value will change depending on how mistaken respondents are told to assume they are. Results would not be useful, because, as Hanemann (1983) has shown, quasi-option value becomes less and less meaningful as assumptions are dropped. Drop the assumption that $d_1 = (0,1)$ and quasi-option value may not be positive. Assume that while information improves over time, some uncertainty will remain and it is questionable whether quasi-option value can be defined in a meaningful way. Assume that active information gathering is possible and the meaning of the concept becomes even less clear.

Conventional cost-benefit analyses become questionable if different degrees of reversibility are present among the alternatives and new information appears to be in the offing. However, this should be addressed directly by procedures which emulate the decision processes of the correct decision maker and not by trying to measure quasi-option values and adding them to benefits. Freeman (1986) correctly argues that the level of analysis is, or ought to be, different for quasi-option value than for option value proper. The latter focuses attention on the individual economic agent as he or she evaluates alternatives under uncertainty. For quasi-option value, the focus ought to be on the public decision maker who is evaluating public policies or projects under uncertainty.

Returning to the quest for theoretically defensible practical welfare measures, note that, if ex ante gainers and losers are assessing the reversibility of the alternatives and informational prospects correctly, this will be reflected in their valuations.

This would seem to reinforce option prices as the correct welfare measure.

Implications for Applied Research

The goal here has been to search the option value literature for theoretical principles to guide empirical research. The concept of option price embodies the principles being sought. It is the applied mirror image of the ex ante compensation test. The alternative of applying the ex post compensation test appeared to be too stringent to be useful in practice. Few if any proposals would have positive net benefits in each and every future state. Use of the expected value of the ex post welfare measures seemed to have little justification in welfare theory. If sufficient contingent claims markets could be established or imitated through public programs, the expected value of the fair bet point would have much to recommend it; but given the poor prospects for such markets, option price is a practical, second-best solution to the valuation problem. Furthermore, option price includes option value whether the latter is positive or negative, large or small. Finally, to the extent that policy alternatives entail different degrees of reversibility and prospects are good for improved information in the future, economic agents will take account of this in determining their individual option prices.

These conclusions can be applied directly in contingent valuation studies. They imply that contingent valuation questions should be directed toward the future. For example, if an environmental improvement project is being evaluated, the valuation question could ask for a hypothetical commitment, to be made before project completion, to pay a certain amount per year for the environmental improvement over the project life or some shorter period. For examples of past studies that correctly implement this procedure see Desvousges et al.,² and Brookshire et al. (1983).

The ex ante compensation test may create greater difficulties for cost-benefit analysis where contingent valuation is not applied. The market prices, which, except for well-understood market imperfections and income effects, reflect social welfare at the margin so nicely in a world of certainty, may not reflect ex ante willingness to pay and accept in an uncertain world.

The problem is not that market prices are necessarily ex post values. Smith (1985) argues that real estate values, wages for occupations with various levels of risk, and other such market prices can be interpreted as ex ante values. Thus, he suggests, it should be possible to derive marginal option prices from hedonic price equations. The problem is that clear division of values into ex ante and ex post values breaks down in the real world. It seems plausible that following Smith's logic would yield an ex ante values; but would they be the correct ex ante values?

²Desvousges, William H., V. Kerry Smith and Matthew P. McGivney. 1983. "A Comparison of Alternative Approaches for Estimating Recreation and Related Benefits of Water Quality Improvements." Washington: U.S. EPA-230-05-83-001, March.

Perhaps the issue can be most easily described through an example. Take a relatively straightforward cost-benefit problem involving electricity, a market good. Suppose the task is to evaluate a hydroelectric dam which, if funded, would be in operation in 1990. Suppose that Mr. Citizen will be a consumer of project electricity and that his demand for the present year is being evaluated as a first step toward projecting his benefits into the future. One can imagine both *ex ante* and *ex post* influences on Citizen's demand at various prices. For example, he may own an air conditioner which he turns on if the weather is hot and does not if the weather is cool. This is an *ex post* demand in the sense that his consumption is determined only after the state of the world (hot or cool) is known. In contrast, Citizen may leave an outside light burning to change the probability of burglary. Because the state of the world (burglary or no burglary) is not known when the electricity for the light is demanded, this must be considered an *ex ante* demand. In this way, both *ex ante* and *ex post* valuations of electricity are incorporated into Citizen's present electricity demand.

Now suppose Citizen's demand has been projected into the future and his willingness-to-pay from the project calculated. Assume for the sake of argument that the projections are accurate. Would the present value of this consumer surplus be an accurate measure of his option price? Applying the *ex ante* compensation test, we would want to ask whether the maximum willingness to pay of Mr. Citizen and others like him would cover the costs of the project. This willingness to pay would have to be evaluated *ex ante*, (e.g., in 1990), with actual demand to be registered in subsequent years. The option value literature seems to imply that these projected values, reduced to present values, would not be fully accurate measures option price. While the projected demands may reflect some *ex ante* considerations, they are, in a sense, not "*ex ante* enough". They do not reflect the same degree of uncertainty that Mr. Citizen faces in calculating his option price for future electricity payable in 1990.

In more general terms, then, market demands may not be fully accurate indicators of the option demands which would have to be measured to fully implement the *ex ante* compensation test. The lack of a full set of contingent claims markets may have ramifications for cost-benefit analysis that are far more serious than most people have recognized. If option prices are a second-best welfare measure then projected consumer surplus measures must be viewed as potentially inaccurate approximations of option prices. They may neglect option values--positive or negative--which reflect differences in the uncertainties consumers would face in arriving at an option price compared to the uncertainty that is reflected in their market decisions. The question then is, "How large are these inaccuracies likely to be?" Large inaccuracies may raise grave questions about the accuracy of cost-benefit analysis generally while small inaccuracies would mean that projected economic surplus values are adequate estimates of option prices.

This brings us back to option value. It was tempting earlier in this paper to discard option value as an irrelevant empirical

concept, because it is option price that is relevant for policy. Now, one might well argue that empirical assessment of option value is a central issue in future attempts to refine cost-benefit analysis. Certainly previously cited contingent valuation studies and those to come in the future will play an important role here; but questions will continue to arise regarding the accuracy of contingent option prices and option values. Thus, Freeman's (1984) semi-empirical look at the sign and size of option value appears to be a pivotal work. The next logical step would be to move from plausible utility functions such as those used by Freeman (1984) to real world people, perhaps in a laboratory or field experiment. It is hoped that option value will turn out to be consistently small. Otherwise, a major rethinking of conventional cost-benefit analysis may become necessary.

Finally, future empirical work would do well to stress implementation of procedures that consider differences in the reversibility of alternative courses of action and prospects for new information. The parallels between conventional cost-benefit analysis and our "mistaken" decision maker are too stark to be ignored. Powerful steps to improve project design and timing and to incorporate active information gathering into the analysis may be in the offing. Such procedures could be directly relevant to many current issues including acid rain, nuclear versus conventional power generation, and hazardous waste disposal.

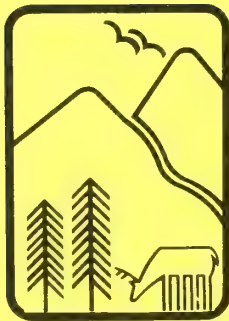
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Considerable progress has been made in recent years in the valuation of non-priced goods. However, emphasis has been on those things most readily measurable. Valuation of wildlife benefits, for example, has aimed at consumptive, on-site recreation use (i.e., hunting and fishing). The danger in these partial estimates of value is that measuring only the on-site consumptive use of wildlife may presume to measure total value. This report examined the task of measuring of-site non-consumptive wildlife values by considering values that include: total value, option value, existence value, quasi-option value, and bequest value. Discrepancies in definitions, measurement problems, and research needs are addressed in this collection of papers.



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